Abrupt Climate Change as an Important Agent of Ecological Change in the Northeast U.S. throughout the Past 15,000 Years

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Abstract (264 words)

We use a series of tests to evaluate two competing hypotheses about the association of climate and vegetation trends in the northeastern United States over the past 15 kyrs. First, that abrupt climate changes on the scale of centuries had little influence on long-term vegetation trends, and second, that abrupt climate changes interacted with slower climate trends to determine the regional sequence of vegetation phases. Our results support the second. Large dissimilarity between temporally-close fossil pollen samples indicates large vegetation changes within 500 years across >4° of latitude at ca. 13.25-12.75, 12.0-11.5, 10.5, 8.25, and 5.25 ka. The evidence of vegetation change coincides with independent isotopic and sedimentary indicators of rapid shifts in temperature and moisture balance. In several cases, abrupt changes reversed long-term vegetation trends, such as when spruce (*Picea*) and pine (*Pinus*) pollen percentages rapidly declined to the north and increased to the south at ca. 13.25-12.75 and 8.25 ka respectively. Abrupt events accelerated other long-term trends, such as a regional increase in beech (*Fagus*) pollen percentages at 8.5-8.0 ka. The regional hemlock (*Tsuga*) decline at ca. 5.25 ka is unique among the abrupt events, and may have been induced by high climatic variability (i.e., repeated severe droughts from 5.7-2.0 ka); autoregressive ecological and evolutionary processes could have maintained low hemlock abundance until ca. 2.0 ka. Delayed increases in chestnut (*Castanea*) pollen abundance after 5.8 and 2.5 ka also illustrate the potential for multi-century climate variability to influence species' recruitment as well as mortality. Future climate changes will probably also rapidly initiate persistent vegetation change, particularly by acting as broad, regional-scale disturbances.

1. Introduction

Current climate trends have induced widespread ecological change including extensive forest mortality (e.g., Kurz et al., 2008; van Mantgem et al., 2009), but the potential ecological outcomes remain uncertain (Adger et al., 2007). Relevant empirical data exist, however, in paleoecological archives like the dense fossil pollen network of the northeastern U.S. (e.g., Williams et al., 2004). Deevey (1939) first recognized that sediment cores from lakes and bogs in the region contained a consistent series of fossil pollen zones, and interpreted them as a record of the ecological response to post-glacial climate change. These zones have been repeatedly documented and are now well dated (e.g., Davis, 1969; Oswald et al., 2007). Deevey's (1939) initial interpretation has also been supported by simulations of the vegetation history (COHMAP, 1988; Prentice et al., 1991) and by comparisons with independent paleoclimate reconstructions (Shuman et al., 2004). The application of these results to ecology and conservation can be enhanced, however, by increasing knowledge about the processes involved in the vegetation response to abrupt and short-lived (100-500 yr) climate changes.

The northeastern U.S. is an ideal location for examining the possible effects of abrupt climate changes because the region was subjected to multiple abrupt changes during the late-Quaternary period. The close proximity of both the Laurentide Ice Sheet (LIS) and the North Atlantic Ocean has made the region's climate sensitive to rapid changes in these features. Many lake sediment records contain evidence of rapid regional climate change, such as when ocean circulation was altered at the beginning and end of the Younger Dryas chronozone (YDC; 12.9-11.6 ka; see Shuman et al., 2002a regarding our use of this term) and when the LIS collapsed at ca. 8.2 ka (Cwynar and Levesque, 1995; Cwynar and Spear, 2001; Huang et al., 2002; Hou et al., 2006; 2007; Kurek et al., 2004; Shemesh and Peteet, 1998; Shuman et al., 2006; Yu, 2007). Holocene climate trends in the North Atlantic region were also punctuated by a series of ice-rafting events (Bond et al., 1997) and by other cool periods documented in Greenland (Alley, 2000). Rapid lake-level changes in the northeast U.S. may be related to these episodes in the North Atlantic (Dieffenbacher-Krall and Nurse, 2005; Li et al., 2007; Newby et al., this volume).

Multiple studies have also indicated that dramatic vegetation changes followed the rapid climate shifts at the beginning and end of the YDC (e.g., Lindbladh et al., 2006; Mott et al., 1986; Peteet, 1990; Shuman et al., 2002a; Yu 2007). These changes exceeded the magnitude and extent of Euro-American land clearance (Shuman et al., 2005a), and may have taken place within 60-150 years (Maenza-Gmelch 1997a; Williams et al., 2002). Other work has highlighted possible vegetation responses to century-scale cool episodes at 8.2 and 13.1 ka (Foster et al., 2006; Shuman et al., 2002b; 2004; 2006; Yu 2007), and to other short-lived climate changes during the Holocene (e.g., Foster et al., 2002).

As a backdrop to the potential abrupt changes, Deevey's (1939) pollen zones represent a dynamic equilibrium between climate and vegetation at millennial and longer timescales. Webb (1986) hypothesized that the equilibrium developed because vegetation responses were short relative to the period of climate change. Each zone has a time-transgressive appearance across the region consistent with slow, orbitally-paced climate change (e.g., Gaudreau and Webb, 1985;

Prentice et al., 1991; Williams et al., 2004), and coincides with a unique combination of temperature and moisture balance favorable to the dominant taxa of the time (Shuman et al., 2004). Even a dramatic decline in hemlock (*Tsuga canadensis*) pollen at ca. 5.3 ka, which was initially thought to be driven only by a pest or pathogen (Davis, 1981), has been attributed to climatic change in the eastern part of hemlock's range (Foster et al., 2006). Indeed, the decline may represent one of the most abrupt responses to climate change in the past 11 kyrs (Calcote 2003; Foster et al., 2006; Haas and McAndrews 1999; Newby et al., 2000; Shuman et al., 2001; 2004; Yu et al., 1997).

Biotic processes and physiographic factors, however, shaped the timing and patterns of the long-term vegetation changes at least locally (e.g., Anderson et al., 1986; Clark et al., 1996; Clark and Royall, 1995; Davis et al., 2005; Green, 1982; Foster et al., 2002; Johnson and Webb, 1989; Lindbladh et al., 2007; Maenza-Gmelch, 1997b; Oswald et al., 2007; Parshall and Foster 2002; Spear et al., 1994; Robinson et al., 2007). Forest modeling studies have shown that tree longevity and successional dynamics could blur the relationship between vegetation and climate at short time-scales, especially when the climatic changes are short-lived or small in magnitude (Davis and Botkin, 1985; Webb 1986). Likewise, some vegetation responses to short-term events such as the Little Ice Age at ca. 0.65-0.1 ka were subtle (Fuller et al., 1998; Parshall et al., 2003). An important question, therefore, remains: how did abrupt climate change influence regional vegetation history and the large ecological response to orbitally-paced climate change (see Shuman et al., 2005a; 2007; Viau and Gajewski 2007)? The answers will illuminate the potential for current and future climate trends to produce slow (e.g., Davis 1989) or rapid (e.g., Williams et al., 2002) changes in vegetation.

Here, we test two hypotheses about the ecological responsiveness to abrupt climate change:

1. *"Slow Response" (SR) – Vegetation history depended primarily upon long-term climate trends*: Vegetation only changed slowly (over >500 yrs) in response to orbitally-paced climate trends. Abrupt changes were only important when subsequent climates lasted substantially longer than the multi-century vegetation response (e.g., during the YDC; Mott et al., 1986);
2. *"Rapid Response"(RR) – Vegetation history reflects the sequence of both abrupt and long climate changes*: Abrupt events directly affected the timing, rates, and direction of vegetation change, even in dense forest, and thus influenced vegetation responses to long-term climate trends.

In the first hypothesis, non-climatic disturbances within a regional forest mosaic (e.g., individual tree mortality, wind-throw, disease, fire) would be the primary mechanism for facilitating the slow replacement of one taxon by another as suited to the climate trends. Disturbances may generate locally-abrupt changes (e.g., Clark et al., 1996; Foster and Zebryk 1993), but regional change was probably only rarely abrupt (e.g., Davis, 1981). In the second hypothesis, abrupt climate changes may favor rapid species declines (e.g., Foster et al., 2006; Shuman et al., 2002a,b), pulses of new species establishment (e.g., Gray et al., 2006; Lyford et al., 2003), the rapid expansion of extant populations (e.g., Foster et al., 2002), and/or changes in evolutionary ecology (e.g., Davis et al., 2005) especially in the presence of widely synchronized disturbances.

Indeed, abrupt climate changes could be considered disturbances themselves. At the scale of the Holocene, abrupt changes may be "discrete" disruptions of ecosystem structure and/or function (cf. White and Pickett, 1985), which affect broad spatial areas (like human land-use; Foster et al., 1998). Current warming trends in the western U.S. have generated such extensive, synchronized disturbances (e.g., Kurz et al., 2008), which will leave important landscape legacies (e.g., Kashian et al., 2005). Similar episodes of climate-induced plant mortality in the past may have been directly forced by climate (e.g., Bigler et al., 2007) or by related variations in regional disturbance regimes (e.g., Clark et al., 1996). Biotic lags may blur (dampen and phase shift) the signals of abrupt events in the pollen data on the scale of centuries (Davis and Bodkin 1985; Webb 1986), but the episodes could directly influence vegetation history by encouraging increases of some taxa and varying the rates of expansion of others (e.g., Jackson and Booth, 2002), enhancing selective pressure on species by rapidly culling the most susceptible individuals (e.g., Boag and Grant, 1981), and altering the long-term trajectory of vegetation change by repeatedly disturbing ecosystems before recovery from prior events was complete (Paine et al., 1998).

This paper applies four tests to these hypotheses based on a series of observations expected from the RR hypothesis, but not from the SR hypothesis. The expectations include episodes of 1) rapid (<500 yr) ecosystem re-organization recorded by high rates of change in fossil pollen data (e.g., Grimm and Jacobson, 1992), 2) synchronous rather than time-transgressive changes in regional vegetation pattern as documented by spatial patterns in the pollen data (e.g., Bartlein et al., 1995; Webb, 1982; Shuman et al., 2002a), 3) coincident rapid climate changes documented by isotopic data and lake-level reconstructions (e.g., Shuman et al., 2004), and 4) equilibrium (or near equilibrium) between short-lived climate conditions and vegetation evident from our ability to use the modern analogs of fossil pollen spectra to reconstruct the abrupt changes (e.g., Overpeck et al., 1985; Prentice et al., 1991). As illustrative examples, we specifically discuss 1) whether the abrupt hemlock decline at ca. 5.3 ka represents a response to abrupt climate change or changes (as allowed by RR hypothesis), or the preferential removal of hemlock by insects or disease (as expected by the SR hypothesis), and 2) the history of chestnut (*Castanea*), which underwent the slowest increase in regional abundance (e.g., Gaudreau and Webb 1985).

2. Methods

2.1. Sites and Age-Depth Models

Our work relies on pollen data from 22 lakes from New York to New Brunswick, which span ~5° of latitude (Fig. 1; Table 1). The sites were chosen for their high temporal resolution and closely-dated stratigraphies from data available from the North American Pollen Database (NAPD), our previous work (e.g., Shuman et al., 2001; 2005b), and additional new datasets made available to us (i.e., from Foster et al., 2006; Oswald et al., 2007). Most 250-yr intervals since 15 ka were directly radiocarbon dated in one or more of the pollen stratigraphies (Fig. 3). The age-depth models for these records are based on linear interpolation between calibrated radiocarbon dates, and derive directly from either the original publications (Foster et al., 2006; Oswald et al., 2007; Shuman et al., 2001; 2005) or the work of Williams et al. (2004) who

generated continental-scale maps of data from the NAPD. We have made no additional changes to any of the chronologies; changes made by Williams et al. (2004) are detailed in Shuman (2001). Given the millennial-scale spacing of most radiocarbon dates used here (Fig. 2), linear interpolation ensures that the age-depth models "cannot deviate too far from reality" (Telford et al., 2004, p. 4) at least near individual dates.

For comparison, we rely on independent paleoclimate reconstructions from four lakes in Massachusetts: Berry Pond (Shuman et al., 2006), Blood Pond (Hou et al., 2006; 2007), Crooked Pond (Huang et al., 2002; Shuman et al., 2006), and New Long Pond (Newby et al., this volume; Shuman and Donnelly, 2006). We use hydrogen isotope data from the first three of these sites, and detailed evidence of lake-level change from New Long Pond. The ages assigned to the isotope data are based on the same linearly-interpolated age-depth models as pollen from the three lakes (Fig. 2), and we use ages for New Long Pond based on Newby et al. (this volume; see more below). Following Telford et al. (2004), we do not entirely rely on linearly-interpolated ages, but 1) ground our conclusions in the calibrated radiocarbon ages that bracket each abrupt event within 500 yrs (Table 2), and 2) use a best-fit approach (rather than linear interpolation) to determine sample ages in one frequently-dated segment of core from New Long Pond. We compare our regional paleoclimate results with Greenland temperature reconstructions (Alley, 2000) and the timing of North Atlantic ice-rafting events (Bond et al., 1997).

2.2. Hypothesis Tests

2.2.1. Test 1: Dissimilarity analyses

Our first test of the two hypotheses relies on dissimilarity analyses of fossil pollen data expanded from Shuman et al. (2005a), and builds on similar earlier studies (e.g., Grimm and Jacobson 1992). Squared-chord distances (SCDs) between fossil pollen spectra separated by 500-yr intervals are used to detect rapid change events in the regional vegetation history. To do so, we first linearly interpolate the pollen data to 250-yr intervals, and then calculate SCDs between every pair of interpolated pollen spectra separated by 500 years in each record. The test works on the premise that vegetation change forced by slow climate trends would not be detectable at sub-millennial scales because the magnitude of change would be small over such short intervals – especially given the longevity of tree species. Shuman et al. (2005a) found that average SCDs across 5000-yr intervals for 15 sites in the northeast U.S. ranged from 0.8 to 0.1, which would reduce to 0.08-0.01 across 500 yr intervals. These values are approximately half or less of the minimum SCD between samples from different biomes today (0.15; Overpeck et al., 1985). Measurements across 500-yr (and even 5000-yr) windows centered on consecutive 250-yr intervals are sufficient to detect responses to climatic step-changes and "oscillations" lasting <500 years (e.g., the 8.2 ka event; Alley et al., 1997) because the measurements span from before to after (and thus encompass) step changes, and from before to during, and during to after "oscillations" (see Shuman et al., 2005a).

As a benchmark of the magnitude of 500-yr vegetation changes, we use the SCD of 0.1, which denotes both the SCDs larger than expected from orbital-scale changes (Shuman et al. 2005a) and the upper 20% of the SCDs across 500-yr intervals measured here. A histogram of the

number of sites per 250-yr interval with SCDs >0.1 shows whether large vegetation changes were evenly distributed or clustered in time (following Bartlein et al., 1995; Webb, 1982). Evenly distributed occurrences of high SCDs would be consistent with the SR hypothesis: abrupt local changes (such as after fires) but progressive regional trends. Simultaneous high SCDs across many sites would be consistent with the RR hypothesis: regionally-extensive and synchronous impacts from abrupt climatic change. We test the significance of peaks in the histogram by iteratively re-sampling the total number of high-SCD occurrences to produce >10,000 synthetic values in 1000 synthetic histograms spanning 14,000 years.

2.2.2. Test 2: Spatiotemporal pattern analysis

Our second test examines the spatio-temporal patterns in the fossil pollen data and associated SCDs to detect time-transgressive versus abrupt spatial shifts in vegetation. We build upon the histogram described above and evaluate whether any temporal clustering of high SCDs (i.e. peaks in the histogram) represent simultaneous changes across >4° of latitude. To do so, we plot SCDs versus time and latitude. We also examine the spatiotemporal patterns of key events within the pollen record (e.g., the timing of the local maxima in spruce and pine pollen percentages) to determine if the timing of these events shifted spatially (as expected from the SR hypothesis) or was temporally clustered (expected in the RR hypothesis). We use histograms of event timing and plots of timing versus latitude to examine the patterns of taxa-specific change (see also Bartlein et al., 1995; Bennett and Fuller 2002; Webb 1982).

2.2.3. Test 3: Independent paleoclimate analyses

Our third test is based on a review of paleoclimate data from the northeast U.S. because the RR hypothesis anticipates similarly timed episodes of abrupt change in pollen, isotope, and lake-level data; the SR hypothesis does not. We consider evidence from outside of the northeast U.S. (i.e., Alley, 2000; Bond et al., 1997), but only in the context of regionally-specific evidence, such as sedimentary hydrogen isotope records (Hou et al. 2007; Shuman et al. 2006). Analytical uncertainty in the isotope data equals <±2‰ (Huang et al., 2002), and we focus only on features in the data represented by more than one sample.

We also use detailed evidence of water-level changes within New Long Pond (41.853°N, 70.679°W; 30-m elevation; 0.14 km^2 area), which is a closed basin in sandy outwash in southeastern Massachusetts (Shuman and Donnelly, 2006; Newby et al., this volume). The evidence of shifts in the position of the lake shoreline through time comes from stratigraphic data in ground-penetrating radar (GPR) profiles of the lake, and from the percent of >63-μm sediments (sand) in contiguous 1-cm interval sub-samples of a series of cores. We infer that the shoreline shifted toward the center of the lake when core sand content was high, and away from the center when sand content was low. X-radiographs and titanium counts from 0.2-mm-resolution core scans on an ITRAX X-ray fluorescence (XRF) corescanner provide supplementary data. AMS radiocarbon dating of macrofossils, and then calibrating the radiocarbon ages using CALIB 5.0 (Reimer et al., 2004), provided age-depth data, which are presented in Newby et al. (this volume).

2.2.4. Test 4: Reconstructions using the modern analog technique

Our fourth test evaluates the prediction of the RR hypothesis that abrupt climate change can be inferred from the pollen data themselves because the events rapidly generated a detectable vegetation response. To test the prediction, we apply the modern analog approach of Overpeck et al. (1985), and use matches between modern and fossil pollen samples to reconstruct past temperature and precipitation trends, as well as the abundance of the individual pollen types.

We specifically use a comparison of observed and reconstructed pollen percentages to evaluate whether the abrupt hemlock decline at ca. 5.3 ka represents a response to abrupt climate change or the preferential removal of hemlock by a pest or pathogen (Davis 1981). The removal of hemlock would alter pollen-climate relationships, and cause observed hemlock pollen percentages after the decline to be lower than anticipated by the modern analog technique. Conversely, if the decline was an equilibrium (community) response to climate change, modern pollen samples should be useful for reconstructing the decline, but climate conditions without a modern equivalent or "analog" could generate error in the analog reconstruction (Jackson and Williams 2004). Additionally, the decline may represent an episode of natural selection because hemlock pollen abundance rapidly declined by >40% from its pre-decline maximum (Allison et al., 1986; Davis, 1981; Williams et al., 2004) and coincided with the preferential removal of hemlock trees from certain edaphic settings (Foster and Zebryk, 1993). Resulting evolutionary change could have altered relationships among hemlock, other taxa, and climate, and thus prohibited modern pollen samples from adequately predicting pre-decline hemlock pollen percentages.

To generate our reconstructions of past climate and pollen trends, matches between fossil and modern pollen samples were made based on SCDs. The SCDs were calculated based on the same list of taxa as used by Shuman et al. (2005a; 2007), but analogs were determined with and without hemlock included in the list. All modern samples from Whitmore et al. (2005) with SCDs of less than 0.3 from an individual fossil sample were considered as analogs of that fossil sample. Most applications of the method (e.g., Overpeck et al., 1985) use lower values than 0.3 (such as 0.15) as the threshold for determining analogs. However, to provide a conservative estimate of whether past hemlock percentages could be reconstructed, we doubled the threshold to allow even weak analogs to be considered. Williams and Shuman (2008) found that thresholds of 0.2-0.3 should be used to maximize the number of samples in a fossil series that can be reconstructed. Reconstructed pollen and climate variables were based on the average of all analogous modern samples; Williams and Shuman (2008) found that doing so would produce low root mean square errors for the reconstructed variables. A representative site-specific reconstruction is shown for the detailed pollen record from Blood Pond, Massachusetts (Oswald et al., 2007), and the results are replicated using all pollen data in the NAPD from before (6ka) and after the hemlock decline (5 and 3 ka).

3. Results

3.1. Test 1 Results: Episodes of high squared-chord distances

Consistent with the RR hypothesis and Shuman et al. (2005a), we find that pollen records from the northeastern U.S. show large, rapid vegetation changes during 500-yr intervals centered on the following times: 13.25-12.75, 12.0-11.5, 10.5, 8.25, and 5.25 ka (Fig. 3). These intervals stand out (e.g., even compared to high SCDs at ca. 11.0, 7.5-7.0, and 6.75 ka) for two reasons: peak occurrences of SCDs of >0.1 at >7 lakes (>90% confidence in the detection of a significant regional change), and peaks in the mean SCD of all sites (Fig. 3). Local SCDs during these intervals were as large as the difference between individual biomes today (0.15), and were as large as during Euro-American land-clearance. The regional-average SCDs for these episodes (except 8.25 ka) were higher than 0.08-0.05, which is the range of distances expected from responses to orbitally-paced climate change (Shuman et al., 2005a).

The high-SCD episodes coincide with the boundaries of regional pollen zones recognized by Deevey (1939) and others (e.g., Davis, 1969; Oswald et al., 2007). Each episode also includes a decline in the pollen percentages of one or more important taxa: pine (*Pinus*) and oak (*Quercus*) at 13.25-12.75 ka, spruce (*Picea*) at 12.0-11.5 ka, pine at 10.5 and 8.25 ka, and hemlock at 5.25 ka (Fig. 3). For example, high SCDs at 13.25-12.75 ka denote rapid increases in spruce pollen percentages (primarily *P. mariana*; Lindbladh et al., 2007) after a decline in pine pollen (primarily *P. banksania*-type; Oswald et al., 2007), and thus mark an important division within Deevey's (1939) A (spruce) pollen zone (Fig. 3). The increase in spruce pollen marks a second spruce peak observed at multiple sites, initially by Leopold (1956), and later attributed to climatic cooling during the YDC (Mott et al., 1986; Peteet et al., 1990).

High SCDs at 12.0-11.5 ka coincide with the end of the YDC, and mark a decrease in spruce pollen percentages at most sites, except some northern sites where spruce pollen percentages climb to a new peak (e.g., Mott et al., 1986)(Fig. 3). Pine pollen percentages also increased at many sites at this time (Shuman et al., 2002b), and pine differentiation indicates that white pine (*P. strobus*) pollen became important (e.g., Lindbladh et al., 2007; Newby et al., 2000; Oswald et al., 2007). The peak in SCDs, therefore, marks the transition from Deevey's (1939) A zone to his B (pine) zone. High SCDs at 10.5 ka denote a decline from the maximum pine pollen percentages recorded at most sites in southern New England (here Massachusetts, Connecticut, and the lower Hudson Valley of New York), and thus the end of the B1 sub-zone described by Oswald et al. (2007).

SCDs peak next at 8.25 ka (Fig. 3) in association with the end of Oswald et al.'s (2007) B3 sub-zone, which temporally extends Deevey's (1939) definition of the B zone to include Davis' (1969) C1a zone and thus the final decline of pine pollen percentages to <20% in southern New England. Many southern lakes record this final – and often rapid – decline in pine pollen percentages after either a plateau or peak in pine pollen percentages (Fig. 3). The B3 zone also includes high *Ambrosia* pollen percentages (Faison et al., 2006), which decline as mesic taxa such as beech (*Fagus*), hemlock, and birch (*Betula*) become regionally important and contribute to the development of new and persistent sub-regional vegetation gradients (Oswald et al., 2007).

High SCDs at 5.25 ka indicate the regional hemlock decline, which was first recognized as a range-wide decline by Davis (1981), and mark an important sub-division within Deevey's (1939) C zone (Fig. 3). The decline does not widely coincide with extensive regional changes in other taxa (Davis 1981), but Foster et al. (2006) and Tzedakis (1992) showed that oak pollen percentages also decline and pine and beech pollen percentages increase at the same time on Cape Cod. Beech pollen percentages also increase at most sites in Maine after 5.25 ka (Fig. 3).

3.2. Test 2 Results: Abrupt changes in spatial patterns

Time-transgressiveness has long been recognized in pollen data from the northeast U.S. (e.g., Gaudreau and Webb, 1985), and is detected here as expected by the SR hypothesis. For example, a long-term decline of pine pollen percentages takes place earlier in southern New England (black lines, Fig. 3g) than in Maine (gray lines, Fig. 3g). Other time-transgressive features of the pollen data include the local timing of the decline of spruce pollen percentages to <5%, the maximum in pine pollen percentages, the rise in beech pollen percentages to >2% (and to >10%, not shown), and the onset of sustained chestnut pollen percentages of >1% (Fig. 4a). At each site, these features have a unique local timing, which is typically later at northern than southern sites (Fig. 4a). Histograms show minimal temporal clustering of these features. Some features, however, have long temporal gaps between occurrences, such as a >1.5 kyr delay in the timing of the decline of spruce pollen percentages to below 5% at the two most northern lakes (at 8.5-8.25 ka in Fig. 3, 4a), and two gaps in the initial local ages of chestnut pollen percentages above 1% at 5.8-3.6 and 2.5-1.1 ka (1 and 2 in Fig. 4a).

In contrast with the expectations of the SR hypothesis, however, the episodes of high SCDs do not show evidence of time transgressiveness over periods longer than ~500 years; high SCDs are not recorded earlier at southern than northern sites. Instead, episodes of high SCDs span >7 sites across >4° latitude within 250-yr bins (Fig. 5), which is consistent with abrupt regional shifts in vegetation composition (like that documented by Bennett and Fuller, 2002; Webb, 1982).

As expected by the RR hypothesis, episodes of high SCDs denote simultaneous abrupt changes in the pollen percentages of individual taxa across >4° latitude. Histograms show the temporal clustering of these features within 250-500 years (Fig. 4b), and indicate "synchronized" regional changes in the biogeography of individual taxa that are an order of magnitude more rapid than the >4000-yr transgressive trends (Fig. 4a). The abrupt or widely synchronous features include the timing of the maximum in spruce pollen percentages at 13.0-12.5 ka, step-like declines in pine pollen percentages at 8.5-8.25 and 8.0-7.75 ka (and again at 6.5 ka at northern lakes), and the hemlock decline at 5.5-5.25 ka. Some abrupt features appear amid time-transgressive trends in the local timing of these same phenomena. For example, the rise of beech pollen percentages to >1% takes place across >4° latitude at 8.25-7.75 ka, and thus punctuates and accelerates a time-transgressive trend from ca. 11-6.5 ka (Fig. 4b). The accelerated trend is evident in maps of beech pollen percentages (Shuman et al., 2002b; Williams et al., 2004). Likewise, the combination of long- and short-term declines in pine pollen percentages (Fig. 3g) illustrates that some abrupt

features may take place more than once locally during related long-term, time-transgressive phenomena (Fig. 6).

Most abrupt features in the pollen record also show spatial differences in character, which are consistent with climatic forcing. For example, Shuman et al. (2002a) documented that conditions in the north during the YDC had been too cold for high spruce pollen percentages, but had been optimal for high spruce pollen percentages to the south. Spruce pollen percentages, therefore, peak in Maine and New Brunswick (gray lines, Fig. 3h) before and after the peaks recorded in southern New England (black lines, Fig. 3h).

Pine pollen percentages undergo similarly contrasting north-south changes at 8.5-8.0 ka (Fig. 6). Four lakes in Maine show evidence of a ~500-yr minimum in pine pollen percentages beginning by 8.25 ka. In contrast, to the south, multiple sites record a final small peak or plateau in pine pollen percentages at 8.5-8.0 ka followed by a rapid decline in these percentages by 7.75 ka. Some important anomalies exist, however, within the regional pattern. For example, high-elevation southern sites such as North and Berry Pond, Massachusetts, record rapid declines in pine pollen percentages at 8.5 ka (Fig. 6c; Shuman et al., 2006), and some sites in Maine (Gould and Unknown Ponds) record peaks in pine pollen percentages at 8.5-8.0 ka. Thus, our histogram of the timing of rapid pine declines (Fig. 4b) shows two clusters of sites recording pine declines across >4° latitude, one at 8.5-8.25 ka and one at 8.0-7.75 ka, and the spatial arrangement of pine pollen percentages throughout the region appears to have shifted both at the beginning and end of the "8.2 ka event" (Fig. 6). Other taxa such as beech also appear to have responded at 8.5-8.0 ka (Fig. 4b), and the brief increase in pine pollen percentages in southern New England coincided with decreases in taxa such as oak (Foster et al., 2006).

The hemlock decline at 5.5-5.25 ka is uniquely consistent across a broad area (Fig. 6), and shows the most tightly clustered range of ages of the events considered here (Fig. 4b). At 5.25 ka, hemlock was not the only taxon to contribute to high SCDs (Foster et al., 2006), but the range-wide decline is unusual in the context of the changes in spruce and pine during the YDC and at 8.25 ka. No north-south contrast in the character of the decline is evident (Fig. 6). The age of the last pollen sample before the decline (excluding one outlier, see below) is similar region-wide (5.47±0.18 ka), as is the age of the first pollen sample after the decline (5.08±0.27 ka). The decline lasted on average 385 years, and its mid-point is 5.28±0.18 ka (ages plotted in Fig. 4b). However, in the highly-resolved pollen record from Spruce Pond, NY, the only abrupt hemlock decline is just above an AMS age of 3.9-3.7 ka (Fig. 6c). The decline combines with a decline in oak pollen percentages and increases in birch and chestnut pollen percentages to generate high SCDs at 4.0-3.75 ka at Spruce Pond and at near-by Sutherland Pond where the hemlock decline is earlier (Fig. 5; Maenza-Gmelch, 1997b); the similar timing of vegetation changes at the two sites and the sequential series of radiocarbon ages from Spruce Pond suggest that the late age of the hemlock decline there is not spurious.

3.3. *Test 3 Results: Abrupt changes in independent paleoclimate evidence*

3.3.1. Isotopic evidence of Pleistocene and early Holocene changes

As expected by the RR hypothesis, hydrogen isotope ratios from palmitic acid (C_{16} *n*-acids), behenic acid (C_{22} *n*-acid), and terrestrial leaf-waxes ($C_{26\text{-}30}$ *n*-acids) record evidence of rapid climate changes at ca. 12.9, 11.6, and 8.2 ka (Fig. 3a,b; Huang et al., 2002; Hou et al., 2006; 2007; 2009; Shuman et al., 2006), as well as at 11.1 and 10.2-10.1 ka (Fig. 3b; Hou et al., 2007; 2009). The palmitic and behenic acid δD data from Berry, Blood, and Crooked Ponds (Fig. 3b) show evidence of the well-documented cooling and warming of the North Atlantic region at the beginning and end of the YDC respectively (e.g., Alley, 2000). The δD value of palmitic acid (δD_{pa}) declines by 17‰ at Crooked Pond at a calibrated radiocarbon age of 13.1-12.9 ka, and the δD value of behenic acid (δD_{ba}) at Blood Pond declines by 24‰ (equal to >5°C) at 12.6-12.1 ka (possibly as early as 13.2-13.0 ka given some radiocarbon dating reversals; Hou et al., 2007; 2009). At the end of the YDC, δD_{pa} data show a 60‰ increase at Crooked Pond just below a calibrated age of 11.3-11.1 ka (Table 2; Huang et al., 2002), and an increase of >7‰ below a calibrated age of 11.3-10.2 ka at Berry Pond (Table 2; Huang et al., 2002). Hou et al. (2007; 2009) inferred a >5°C increase in temperatures at 11.3-11.2 ka from a >20‰ increase in δD_{ba} at Blood Pond. These lines of evidence indicate rapid regional cooling when pine pollen percentages declined and SCDs were high at 13.25-12.75 ka, and rapid regional warming when spruce pollen percentages declined and SCDs were high at 12.0-11.0 ka (Fig. 3). Sedimentary and chironomid data support this interpretation (e.g., Cwynar and Mayle, 1995; Levesque et al., 1997; Shuman et al., 2004), as do the relative position of isotopic and pollen stratigraphic features within individual cores (e.g., Huang et al., 2002; Hou et al., 2007).

Hou et al. (2007; 2009) inferred brief drops in annual temperatures of ~3-4°C at 11.1 ka and 10.2-10.1 ka (Fig. 3b) when Newby et al. (this volume) find evidence of regional drought and when numerous pollen stratigraphies have high SCDs (Fig. 3d). The temporal detail of the Holocene portion of the Berry Pond δD_{pa} data also reveals a negative anomaly of 10‰ at 8.7-8.1 ka (Table 2), which is associated with features in the Berry Pond pollen stratigraphy similar to those dated to after 8.3 (8.6-8.0) ka at near-by North Pond (Shuman et al., 2006). These pollen stratigraphic features include rapid declines in pine pollen percentages (Fig. 6c) and other features that contribute to the regional peak in SCDs at 8.25 ka (Fig. 3, 4). Likewise, a deviation from long-term δD trends is also evident at Berry Pond at ca. 7.5-7.0 ka (Shuman et al., 2006) when 6 sites record high SCDs (Fig. 5).

The δD values of multiple leaf-waxes extracted from sediments at Berry and Crooked Ponds record a similar and rapid step-like shifts of >20‰ at ca. 10.5 and 8 ka (Fig. 3a; Shuman et al., 2006). The first of these shifts is dated within 500 years at both lakes (Fig. 2). The age range of the second shift at Crooked Pond overlaps with the inferred age range at Berry Pond, but neither record is well constrained by calibrated radiocarbon dates except a date of 7.7-7.6 ka above the shift at Crooked Pond (Table 2). The close relative position of the isotopic shift and the pine pollen decline within the individual cores is consistent with the inference that rapid climate and vegetation changes were concurrent (Shuman et al., 2006). Shuman et al. (2006) interpreted the shift as the result of seasonal precipitation changes following the collapse of the LIS at 8.2 ka. Hou et al. (2006) used different isotopic measurements from Blood Pond to infer a

similarly-timed step change in humidity, which coincides with increased importance of mesic taxa such as beech.

3.3.2. Evidence of Holocene lake-level changes

The sedimentary data (Fig. 6-8) from New Long Pond, Massachusetts, are also consistent with the RR hypothesis, and show evidence of repeated low lake-stands (droughts) during the Holocene – as well as during the late-Pleistocene (Newby et al., this volume) – that are associated with variability in the pollen data. GPR data show five major stratigraphic units within the lake-basin (Fig. 7a), including two prominent paleoshorelines (associated with units B and D) dated by Shuman and Donnelly (2006) to 10.5-9.4 ka and after 5.7-5.4 respectively.

The upper of these two GPR units (D) can be sub-divided into at least seven sub-units associated with bright reflectors and near-shore unconformities (Fig. 7a). By contrast, the bounding units (C and E) do not show strong sub-divisions and contain fine-grained sediments (dark in the GPR profile), which extend further shoreward than those in unit D.

Grain-size data from a core (NLP43), which spans GPR units C-E, shows that the unit D sub-divisions coincide with layers of high sand concentration from 5.7-1.3 ka (Fig. 7b). By contrast, older sediments dating from 8.9-5.7 ka in NLP43 have low sand content, except in association with a calibrated radiocarbon age of 8.5-8.4 ka (Table 2). A >30-cm layer of continuous, visible sand, which comprises unit D in core NLP31, also dates from before 5.3 ka to 2.2 ka, is overlain by a second sand layer before 1.3 ka, and lies above a unit of massive organic-rich silts (Fig. 7b).

Important for our hypothesis test, the episodes of sand deposition, which we infer to represent periods of low water-levels during drought (see also Newby et al., this volume), correspond in time with abrupt shifts in pine and hemlock pollen percentages (Fig. 6b,c). A correlation with low temperatures in Greenland is also similar to the most severe historic drought in the northeast U.S. (in AD 1964-1966; see Newby et al., this volume). Conditions analogous to this severe historic drought thus coincided repeatedly with low hemlock pollen percentages at coastal pollen records near New Long Pond (Fig. 8a). The similarity improves when an autoregressive moving average of the preceding 300-1000 years is calculated from the grain-size data (Fig. 8b). The moving average of the grain size data replicates the low-frequency (>500 yr) aspects of the hemlock pollen data, including the period of low hemlock pollen percentages from ca. 5.5 to 3.3 ka. The three periods with the lowest hemlock pollen percentages (0-0.5%) after 5.5 ka (a, b, and c in Fig. 8) are also similar in time to peaks in the moving average of the grain-size data.

3.4. Test 4 Results: Reconstructed abrupt climate and vegetation changes

3.4.1. Pollen-inferred abrupt climate changes

Consistent with the RR hypothesis, the modern analog technique was able to reconstruct abrupt climate changes. Large temperature changes are inferred at the beginning and end of the YDC based on the detailed pollen record from Blood Pond, Massachusetts (Oswald et al., 2007), just as has been done for other records from the region (e.g., Shuman et al., 2007; Viau and Gajewski

2007). The character of temperature changes at 12.9 and 11.6 ka, however, is not as abrupt as in the isotopic data (compare Fig. 3 and 9). Other abrupt changes in the reconstruction include steps in annual precipitation at 9.5-9.1 ka (+170 mm/yr), 8.0-7.7 ka (+95 mm/yr), and 2.0-1.9 ka (+40 mm/yr), when small steps in temperature (~1-2°C) were also inferred (Fig. 9a). The step changes at ca. 8.0 and 2.0 ka coincide in time with precipitation changes inferred from leaf-wax δD data (Fig. 3a; Shuman et al., 2006) and the top of a dense layer of sand in core NLP31 (Fig. 7b). When hemlock is included in the pollen sum, we also infer multi-sample declines in annual precipitation (-90 to -120 mm/yr) associated with cool episodes at 6.3-6.0, 4.7-4.6, 3.7-3.3, 2.6-2.0, and 1.2-1.1 ka. Several of these episodes are similar in timing to episodes of high sand content in NLP43 at 6.1-5.6, 4.7-4.4, 2.4-1.9, and 1.4-1.2 ka, but the correlation is weak (Fig. 8b,c) and the magnitude of the reconstructed droughts is similar to our uncertainty (±135 mm; Williams and Shuman 2008).

Another important aspect of the reconstruction is a rapid decline in the quality of the analogs (with and without hemlock in the pollen sum) after 8.0 ka (Fig. 9b). The SCDs associated with the best analogs for each sample from 7.8-2.2 ka are >0.15, which is the threshold that Overpeck et al. (1985) used to separate samples from different biomes.

3.4.1. Error in the reconstruction of the hemlock decline

Leaving hemlock out of the analog matching process at Blood Pond causes the reconstructed and observed trends in hemlock pollen percentages to differ substantially (Fig. 9c). High percentages of hemlock pollen before ca. 5.5 ka were not reconstructed even though the only noticeably large effect on the climate reconstructions is in the character of precipitation trends in the last 2 kyrs (Fig. 9a). A similar effect is also evident in a mismatch between reconstructed and observed beech pollen percentages until ca. 2 ka.

Just as at Blood Pond, high hemlock pollen percentages are not reconstructed across eastern North America before the decline when hemlock is left out of the analog-matching process (Fig. 10). Reconstructed hemlock pollen percentages vary from 0 to 12% at 6 ka, but the observed values range from 0 to 50%. The percentages of hemlock pollen are under-predicted at other times as well (see also Prentice et al., 1991), but 60.8% of cases at 6 ka are under-predicted compared to 24.7% at 5 ka and 34.4% at 3 ka. The number of good matches (residuals of 2% to -2%) also increases from 29.5% of cases at 6 ka to 47.0% of cases at 3 ka. Even with hemlock used in analog matching, observed values as high as ~60% are under-predicted in the reconstructions as values of ~20% or less. Few modern pollen samples (possible analogs) contain the high hemlock percentages observed at 6 ka (Williams et al., 2006).

4. Discussion

4.1. Vegetation responses to abrupt climate changes

Like others (e.g., Gaudreau and Webb 1985), we observe multiple time-transgressive features in the regional pollen data (Fig. 4a), and local changes that include long-term (rather than abrupt) changes in the abundance of the individual taxa (e.g., declines in pine pollen, Fig. 3). Our tests, however, consistently produced additional observations consistent with the predictions of the

RR hypothesis (importance of abrupt changes) and conflicting with the SR hypothesis (the dominance of slow, long-term changes). Individuals of one taxon (e.g., oak) probably replaced those of another (e.g., pine) slowly within the shifting regional mosaic of disturbance (e.g., individual tree mortality, wind throw) as climate trends slowly shifted, but abrupt climate changes punctuated and influenced this pattern of replacement by generating vegetation changes that were at times as extensive and dramatic as Euro-American land-clearance (Fig. 5).

Indeed, five of Deevey's (1939) pollen zone boundaries – or sub-zone boundaries recognized later (e.g., by Davis, 1969; Oswald et al., 2007) – are associated with 1) peaks in SCD values indicating rapid vegetation change, 2) widespread rapid changes in the relative abundance of individual taxa, 3) independent (albeit sometimes weakly dated) evidence of rapid paleoclimate changes (e.g., at the beginning and end of the YDC; at ca. 8.25 ka; after 5.7 ka), and 4) step-changes in climate variables reconstructed from the pollen data. All of these observations were predicted by the RR hypothesis. Several repeated results include the observation that the inferred abrupt vegetation changes bound or punctuate the time-transgressive vegetation trends (Fig. 3, 4), and coincide with abrupt declines in the pollen percentages of major taxa: pine at 13.0-12.5 ka (largely *P. banksiana*-type; see Oswald et al., 2007), spruce at 12.0-11.5 ka (largely *P. mariana*; see Lindbladh et al., 2007), pine at 8.5-7.75 ka (largely *P. strobus*-type; see Oswald et al., 2007), and hemlock at 5.5-5.25 ka. These declines were then followed by increases in the importance of other taxa (e.g., pine after 12.0-11.5 ka; beech, birch, and hemlock after 8.25 ka; Fig. 3). The peak abundance of individual taxa also shifted spatially following several abrupt changes, such as recorded by north-south contrasts in the direction of change in spruce and pine pollen percentages at 13.0-12.5 and 8.5-8.25 ka respectively (Fig. 3, 5).

The independent evidence of abrupt climate change (e.g., Fig. 3, 7) backs the inference that the abrupt vegetation changes were not generated by rapid ecological processes alone. In fact, rapid vegetation change appears to have only been regionally extensive when we independently infer abrupt climate events (Fig. 3, 8). The inferred rapid change events typically correspond in time with documented ice sheet and oceanic dynamics, such as during the YDC (Clark et al., 2001) and at ca. 8.2 ka (Barber et al., 1999). Alley (2000) reconstructed low temperatures in Greenland during several of the rapid vegetation episodes (e.g., Fig. 6a), and the 5.8-5.2-ka age of the most prominent ice-rafting episode recognized by Bond et al. (1997) overlaps with the most-common age of the hemlock decline at 5.5-5.25 ka. Five ice-rafting episodes overlap in time with episodes of high SCDs (Fig. 4), and another five overlap with periods of high sand content in NLP43 (Fig. 7; Table 2).

That these abrupt regional climate changes can be reconstructed from the fossil pollen data (Fig. 9) reduces concerns about substantial lags in the biotic response (Davis, 1989). To produce such reconstructions, the pollen data must capture a response to each of the abrupt climate events on the scale of decades to centuries (e.g., Williams et al., 2002) rather than over many centuries and longer. Even century-scale droughts inferred from sedimentary data at New Long Pond appear weak but potentially detectable in the pollen-based precipitation reconstruction (Fig. 8c).

Given the time span of each inferred drought, the ratio of vegetation response time (~300-yr tree longevity and successional dynamics) to the period of climate change (e.g., 125-310 yr droughts) is large (2.40-0.97) compared to the ratios for orbital-scale changes (~300 yrs/11,000 yrs). Based on theory presented by Webb (1986), the large response/forcing ratios correspond to an 80% reduction in the amplitude of the biotic responses and phase lags of ~80° (~30-70 yrs). Similarly, the ~100-mm amplitudes of reconstructed droughts at Blood Pond since 8.0 ka (Fig. 8c) appear reduced because they equal only ~10-50% of the magnitude of a severe drought in AD 1964-66, which left a sedimentary signature at New Long Pond similar to the evidence for multi-century droughts in the mid-Holocene (see Newby et al., this volume for more detail). The expectation of multi-decadal lags is consistent with the determination of 60-100 yr lags following abrupt temperature changes during the YDC (William et al., 2002), and helps to demonstrate the temporal scales applicable to the RR hypothesis. Future studies are needed that combine well-dated high-resolution paleoclimate reconstructions with detailed (sub-centennial) pollen counts, because they will enhance understanding of the potential dynamics involved (e.g., relative rates of tree mortality) involved in strong versus weak responses to abrupt events.

4.2. Abrupt climate change as multi-century, broad-scale disturbance

In many cases, the detailed signal of abrupt events may be one of extensive ecosystem disturbance (Marlon et al., 2009). Like broad-scale human land-use (e.g., Foster et al., 2003) and other large disturbances (e.g., Kurz et al., 2008), abrupt climate changes appear to have caused extensive declines in individual tree taxa (e.g., *Picea glauca* at 12.0-11.5 ka; *Pinus strobus* at 8.25 ka; hemlock at 5.25 ka), which coincided with and likely facilitated increases in the abundance of others (e.g., *P. strobus* at 12.0-11.5 ka; beech at 8.25 ka). Other weaker climate changes (e.g., during the Little Ice Age at ca. 0.65 ka) may not have been sufficiently large or rapid to extensively disturb the forests, and thus were not detected by our methods.

The abrupt changes that we detected, however, meet the definition of disturbance as "discrete" events that disrupted ecosystem structure and/or function, as well as composition (White and Pickett, 1985). These disturbances then also generated legacies (cf. Foster et al., 2003) that influenced the subsequent response to slow, orbitally-pace climate change (i.e., Deevey's pollen zones). For example, the hemlock decline affected both ecosystem structure (e.g., Fuller, 1998) and function (e.g., St. Jacques et al., 2000), and corresponded locally to regionally with persistent increases of other taxa, such as chestnut (see Maenza-Gmelch, 1997b) and beech (Fig. 3; Foster et al., 2006). Foster and Zebryk (1993) describe the initial succession of hemlock by black gum (*Nyssa*) following the decline in central Massachusetts, and then the persistence of black gum through the remainder of the Holocene. These inferences lead to related predictions that need to be examined: highly-resolved pollen data and biogeochemical data (e.g., McLauchlan et al., 2007) may detect trends driven by successional processes if mortality and species replacement were widely synchronized across pollen-source areas or watersheds (i.e., not part of heterogeneously-aged landscape mosaics).

Just as recent variations in landscape structure and composition associated with large disturbances such as fire can diminish over several centuries (e.g., Kashian et al., 2005), the

effects of some climate events (e.g., at 7.5 ka) may not be long lived if the subsequent climate favored the species that were initially present. Ecological resilience (i.e., the potential for the regional vegetation to return to a given configuration after a perturbation; Biesner et al., 2003) may have been exceeded, however, when an event coincided with 1) the development of new and persistent climatic conditions or 2) additional abrupt events within the time frame of the initial biotic response (see Green 1982; Paine et al., 1998). Note that the modern analog technique reconstructed step changes in temperature or precipitation at Blood Pond during many of the major abrupt events (Fig. 9), and that hydrogen isotope data show step changes at ca. 13.0, 11.5, and 8.25 ka (Fig. 3a,b). Furthermore, evidence of rapid lake-level changes at New Long Pond indicates repeated abrupt events after ca. 5.7 ka (Fig. 7).

4.3. The distinctive and illustrative response of hemlock

The range-wide decline of hemlock pollen percentages in the mid-Holocene is unique, and may be illustrative of the long-term ecological and/or evolutionary influence of frequent or repeated abrupt climate events. High SCDs widely indicate the decline (Fig. 3, 5), which represents a rapid re-organization of spatial patterns (Fig. 4-6) and is associated with the first and possibly most severe of a series of droughts inferred from sedimentary evidence (Fig. 6, 8). However, the broad pattern of decline differs from previous declines of spruce and pine (Fig. 3, 6) because spruce and pine increased elsewhere at 12.0-11.5 and 8.5-8.25 ka respectively (Fig. 3, 6). The spatial pattern of climate change at ca. 5.5 ka may also differ from earlier abrupt events, but no evidence exists for a large geographic shift in the distribution of hemlock (see e.g. Williams et al., 2004).

A disease or pest outbreak (e.g., Davis 1981; Bhiry and Filion 1996) remains a plausible explanation for the unique pattern of decline, but several observations raise the possibility that the importance of such an agent should be re-evaluated. First, moving averages of the New Long Pond grain size data show that autoregressive processes could transform a period of high variability into a low-frequency pattern like that observed in the hemlock pollen data (Fig. 8). If so, a disease or pest outbreak may not be required to explain the decline, and range shifts (such as associated with changes in other taxa) would not enable hemlock to "escape" the variability. Thus, like a disease, climatic variability could produce a decline in abundance across a range determined by other climatic factors (e.g., minimum temperatures; mean precipitation).

The persistent decline could have been initiated by the most severe of several droughts (either episode a, b, or c in Fig. 8) and then sustained by subsequent droughts that prohibited hemlock's full recovery (as described by Paine et al., 1998). Tree longevity and population dynamics (e.g., the dependence of seed production and banking on prior population levels and their fecundity) would allow hemlock pollen percentages at any given time to depend on the average or net moisture level of the preceding 300-1000 years. Repeated, drought-induced disturbance and autoregressive succession dynamics from ca. 5.5-2.0 ka may also parallel those in fire-prone ecosystems (Green 1982); persistent "disequilibrium" could explain the weak reconstruction of drought using modern analogs (Fig. 8c) and the simultaneous period of unusually low SCDs (i.e., repeated droughts maintained the disturbed state of the vegetation

681 rather than initiating large, new changes; Fig. 2c,d). Evidence for variable moisture availability
682 (i.e., repeated droughts) after 5.7 ka also comes from Ontario (Haas and McAndrews 1999) and
683 the Wisconsin-Michigan border (Ewing 2000). Lags of 1000 years, however, seem extreme in the
684 context of data that capture repeated responses to other 100-300 year long climate changes, and
685 the correlation probably also indicates the importance of low-frequency moisture trends (e.g.,
686 Shuman and Donnelly, 2006).
687
688 Second, the contrast between the tight clustering of ages among most sites considered here
689 (5.47±0.18 ka; Fig. 4b) and the much later (3.9 ka) directly-dated age of the decline at Spruce
690 Pond, NY (Fig. 6c; Maenza-Gmelch, 1997b) raises the possibility that the decline is not as
691 synchronous across its range as previously inferred (Davis, 1981; Webb 1982). Bennett and
692 Fuller (2002) also found multiple modes in their analysis of the age of the hemlock decline. The
693 most prominent mode dates to 5.595 ka, but other modes include ca. 7.4, 5.8, 5.1, and 4.5 ka.
694 Such scatter may be anticipated in empirical data, but others have described repeated drought-
695 related hemlock declines at ca. 5.7 and 5.1 ka (Haas and McAndrews 1999) and two episodes of
696 phytophagous-insect damage on hemlock needles at 5.8-5.5 and 4.9-4.6 ka (Bhiry and Filion
697 1996; see also Anderson et al., 1986). The range of ages could be inconsistent with the spread of
698 a disease within decades (Allison et al., 1986), and may instead indicate that patchy local-to-
699 regional declines resulted from the local severity of different droughts (Fig. 6).
700
701 Third, our inability to use modern analogs to reconstruct the decline (or to over-predict hemlock
702 pollen percentages after the decline; see section 2.2.4) could indicate that the decline represents
703 a response to climatic conditions without a recent equivalent. Important for the premise of this
704 paper, a climate distinctive for its high variability at century timescales, such as inferred from
705 the New Long Pond GPR and grain-size data (Fig. 7), may have contributed to the lack of good
706 analogs. Step shifts and subsequent declines both in leaf-wax δD values (Fig. 3a) and analog
707 SCDs at Blood Pond (Fig. 9b) also suggest the importance of seasonal precipitation changes (see
708 e.g., Shuman et al., 2006). The end of "no-analog" conditions with large seasonal temperature
709 contrasts led to long-term declines of elm (*Ulmus*) and ironwood (*Ostrya*-type) in the early
710 Holocene (e.g., Delcourt and Delcourt 1994; Jackson and Williams, 2004), but the modern
711 distribution of hemlock falls well within the range of seasonal temperatures that exists today.
712 Instead, the abundance of hemlock (and beech which is also poorly reconstructed; Fig. 9) would
713 be susceptible to small changes in the combination of temperature and precipitation (Fig. 11; see
714 also Calcote 2003).
715
716 Finally, natural selection may have been an additional autoregressive "filter" on hemlock pollen
717 percentages. Modern analogs under-predicted the pre-decline percentages (Fig. 10c), but the
718 differences between post-decline percentages and their analogs were commonly -2 to 2%. Such a
719 result was anticipated for a case of rapid natural selection, which could have resulted given that
720 the prominent decline resulted from either the culling of many individuals (mortality selection)
721 or from reduction in the average pollen productivity of the individuals (fecundity selection)
722 across a large region and pollen source area within the life span of individual trees at 5.25 ka.

Even if some areas experienced declines at different times, the decline is the most rapid and most-commonly synchronous vegetation change in the region (Fig. 4b). Individuals buffered from either mortality or reduced fecundity would then have had a reproductive advantage after the decline. For example, individuals in populations from moist micro-sites recovered more quickly than those on dry upland sites (Foster and Zebryk 1993), and could have had a mating (i.e., pollen dispersal) or establishment (i.e., seed production) advantages. A resultant evolutionary shift may have changed hemlock's relationships with climate and other taxa. The modern relationships therefore only developed after the decline when hemlock pollen percentages were most accurately reconstructed (Fig. 9, 10).

4.4. Abrupt events and chestnut

The regional history of chestnut illustrates that abrupt changes may have also meaningfully interacted with the effects of long-term climate trends even when they did not involve rapid local changes (detected by high SCDs). Chestnut abundance increased throughout the northeast U.S. as conditions shifted toward a cool, wet climate (e.g., Shuman et al., 2004), but the increase appears to have repeatedly stalled given gaps in the time-transgressive timing of chestnut pollen percentages at >1% (Fig. 5a). These gaps are longer than observed in the time-transgressive trends of other taxa, which suggests that site density may not be a factor. Additionally, the gaps (from 5.8-3.6 ka and 2.5-1.1 ka) correspond both with periods of low chestnut pollen percentages in individual records (e.g., Rogers Lake, Davis, 1969) and droughty intervals inferred at New Long Pond (Fig. 8b) and elsewhere (Muller et al., 2003). Extant populations remained through the gaps, but only expanded or colonized new and even near-by sites after abrupt climatic changes (e.g., Foster et al., 2002; Maenza-Gmelch, 1997b). Abrupt changes, therefore, were not simply episodes of extensive disturbance. Interactions among climate variability, physiography, and seed dispersal (like the processes noted by H. D. Thoreau; Foster et al., 2002) may also be important (Gray et al., 2006; Lyford et al., 2003), and the role of metapopulation dynamics (e.g., Levin and Clay, 1984) needs to be examined.

5. Conclusions

Our tests support the hypothesis that the vegetation history of the northeastern United States depended on the specific sequence of both long-term and abrupt climate changes over the past 15 kyrs. We find evidence of 1) synchronous, rapid changes in vegetation composition across >4° latitude, and 2) coincident abrupt regional climate changes. These observations indicate that abrupt climate changes superimposed periods of rapid ecosystem reorganization upon long-term time-transgressive changes, and are thus inconsistent with the hypothesis that slow (>500 year) responses to long-term climate trends alone produced the regional vegetation history.

Abrupt climate changes at 13.25-12.75, 12.0-11.5, 10.5, 8.25, and 5.25 ka appear to have been sufficiently large to act as broad, regional disturbances, and often generated rapid species declines. Some abrupt events stalled or reversed the long-term trends, such as during the YDC or when regional cooling at ca. 8.5-8.25 ka briefly delayed the final decline of pine populations in southern New England. Abrupt events also accelerated some long-term trends, such as when rapid regional change at 8.25-8.0 ka enhanced the regional increase in beech abundance. Finally,

some combinations of abrupt events probably uniquely altered the trajectory of regional vegetation trends. In particular, regional hemlock abundance declined after ca. 5.5 ka during a period as unique for its climatic variability as other periods are for their combinations of mean temperatures and precipitation. Like the distinctive vegetation history of areas repeatedly perturbed by fire (e.g., Green 1982), low hemlock abundance from 5.5 to 2.0 ka may represent a period of autoregressive responses to repeated droughts, possibly including effects of natural selection on the linkage between hemlock and climate. Likewise, the history of chestnut indicates that multi-century climate variability was important even in the absence of enhanced disturbance, and imposed controls on recruitment and population expansion that also influenced vegetation history.

Overall, past abrupt climate changes have been as dramatic an agent of ecological change in the northeastern U.S. as Euro-American land clearance (Fig. 3, 5). The past changes underscore the potential for current and future climate trends to effect dramatic vegetation change as well, especially given the broad disturbances now affecting some ecosystems (e.g., Kurz et al., 2008). Global ecological outcomes will likely depend on the rate and magnitude of future climate trends, and thus the ability of the trends to further disturb large areas of vegetation.

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Figure Captions

Figure 1. Site Map. Locations of the 22 pollen records used in this study are shown and labeled as listed in Table 1. States in the northeast U.S. are labeled in gray: New York (NY), Connecticut (CT), Rhode Island (RI), Massachusetts (MA), Vermont (VT), New Hampshire (NH), and Maine (ME).

Figure 2. Radiocarbon dates for the 22 pollen records used here. A) Histogram showing the number of sites with a calibrated radiocarbon dated (used in its age-depth model) at each 250-yr interval. B) Calibrated median and 1σ age-range for each point in the age-depth model of a given sites. Radiocarbon dates (black), radiocarbon ages adjusted for old-carbon effects (open), pollen stratigraphic ages (gray) and core-top ages (gray) are shown. Sites are listed by latitude; sites with isotopic data are in bold.

Figure 3. Hydrogen isotope data from organic sedimentary compounds at Berry, Blood, and Crooked Ponds, Massachusetts (A, B; Huang et al., 2002; Hou et al., 2007; 2009; Shuman et al., 2006) compared with (C) a histogram of the number of records with high dissimilarity values per 500 yr interval (>0.1 squared-chord distances, SCDs) and (D) the individual dissimilarity time-series from all of the records (dashed lines). Time series of the pollen data from each site are shown to the right (E-H). Gray bars mark intervals of large change in the pollen data as estimated by coincident peaks in the histogram (in C) of the number of sites with high SCDs per 250-yr interval and in the mean regional SCD (thick black line, D). Palmitic acid δD values (B; C_{16} n-acid δD) from Crooked and Berry Ponds were increased by 40‰ VSMOW to plot on the same axis with behenic acid δD values (gray in B, C_{22} n-acid δD) from Blood Pond.

Figure 4. Latitudinal plots and histograms of A) time transgressive and B) abrupt changes in individual pollen taxa. A). The latitudinal plots and histograms (from top to bottom) show the transgressive timing of the pollen percentages of chestnut (*Castanea*) rising consistently above 1%, beech (*Fagus*) rising consistently above 2%, pine (*Pinus*) reaching their local maximum, and spruce (*Picea*) declining to below 5%. Circled numbers indicate two gaps in the spread of chestnut pollen percentages above 1%. B). The latitudinal plots and histograms (from top to bottom) show the widely-synchronous timing of the hemlock (*Tsuga*) decline, the rise of beech pollen percentages to consistently above 1%, all rapid declines in pine pollen percentages, and the local maximum of spruce pollen percentages. Dashed lines mark the level of four sites per 250-yr interval in the histograms.

Figure 5. Histogram and latitudinal plot of squared-chord distances (SCDs). The black histogram (top) shows the number of sites per 250-yr interval with SCDs >0.1; horizontal lines indicate the significance of histogram peaks based on iterative re-sampling of the data. The regional mean SCD is also shown as a line (top). Bubble size (bottom) indicates the SCD value (the largest bubbles indicate SCDs >0.5; the smallest, SCDs <0.025), and bubble location indicates age and site latitude.

Figure 6. Pine (*Pinus*) and hemlock (*Tsuga*) pollen percentages compared to paleoclimate data. A) Percent sand in a core from New Long Pond (NLP43; see Fig. 7) and reconstructed temperatures from Greenland (Alley 2000) are plotted versus time for 10.0-6.0 ka (left) and 6.5-3.6 ka (right). Detailed pollen diagrams show contrasts in the direction of change in pine pollen percentages (left) in B) Maine and C) southern New England, but no similar contrast for hemlock pollen percentages (right). Different line styles indicate different pollen sites noted on the right; *denotes sites from Maine plotted with those from southern New England.

Figure 7. GPR and grain-size data show evidence of repeated periods of lake levels at New Long Pond, Massachusetts. The GPR data (A) contain five stratigraphic units (A-E), and units D represents a mid- to late-Holocene interval when multiple reflectors (horizontal white bands) indicate repeated low lake-levels. Core data from two cores collected near the shore of New Long Pond (NLP). Sand layers (paleoshorelines) are evident as light colored bands in a photograph of core NLP31 and an x-radiograph of core NLP43; core numbers indicate distance from shore in meters. XRF counts of titanium (Ti) are shown to the right of each image and grain-size data (percent dry mass of the >63 μm fraction) is shown to the left of the NLP43 radiograph. Black dots represent the location and calibrated (calendar year before AD 1950) ages of AMS radiocarbon analyses (see Newby et al., in review for data).

Figure 8. The hemlock pollen data (A) show declines during the droughts inferred from grain size data at New Long Pond (B) and less clearly from a pollen-inferred precipitation reconstruction from Blood Pond (C). The sand-content data shown here come from NLP43 (see Fig. 7 and Newby et al., this volume), and are also presented as running averages of the preceding 300 (dotted line, B) and 1000 years (black line, B). Three episodes of inferred drought and low hemlock pollen percentages are labeled (a, b, c). Pollen data come from Rogers Lake, Connecticut (black circles, Davis, 1969), Winneconnet Pond, Massachusetts (black diamonds, Suter, 1985), and Deep Pond (open circles, Foster et al., 2006). Gray bars mark periods of low hemlock pollen abundance.

Figure 9. Pollen-inferred paleoclimate reconstructions (A), SCD of the best analogs (C) and pollen (B) data from Blood Pond, Massachusetts (Oswald et al., 2007). Gray lines show values of mean July temperature, annual precipitation, and pollen percentages reconstructed using the modern analog technique without hemlock pollen included in the analog matching process. For comparison, the observed pollen percentages are shown in black, and climate reconstructions based on the modern analog technique including values of hemlock pollen percentages are shown in black.

Figure 10. Histograms of A) observed versus B) reconstructed hemlock (*Tsuga*) pollen percentages from all sites in the North American Pollen Database in eastern North America at 6, 5, and 3 ka. Residuals (C) are shown at the bottom.

Figure 11. Modern climate-hemlock pollen relationships. Light gray symbols represent all of the locations of North American pollen surface samples in the Whitmore et al. (2005) modern

pollen-climate dataset; darker symbols indicate areas with eastern hemlock (*Tsuga* spp.) occurrence. Hemlock occupies an area well within the available "climate space" on a plot of January versus July temperatures, but is near the margin of the "climate space" defined by July temperature and annual precipitation (precip).

Figure 1

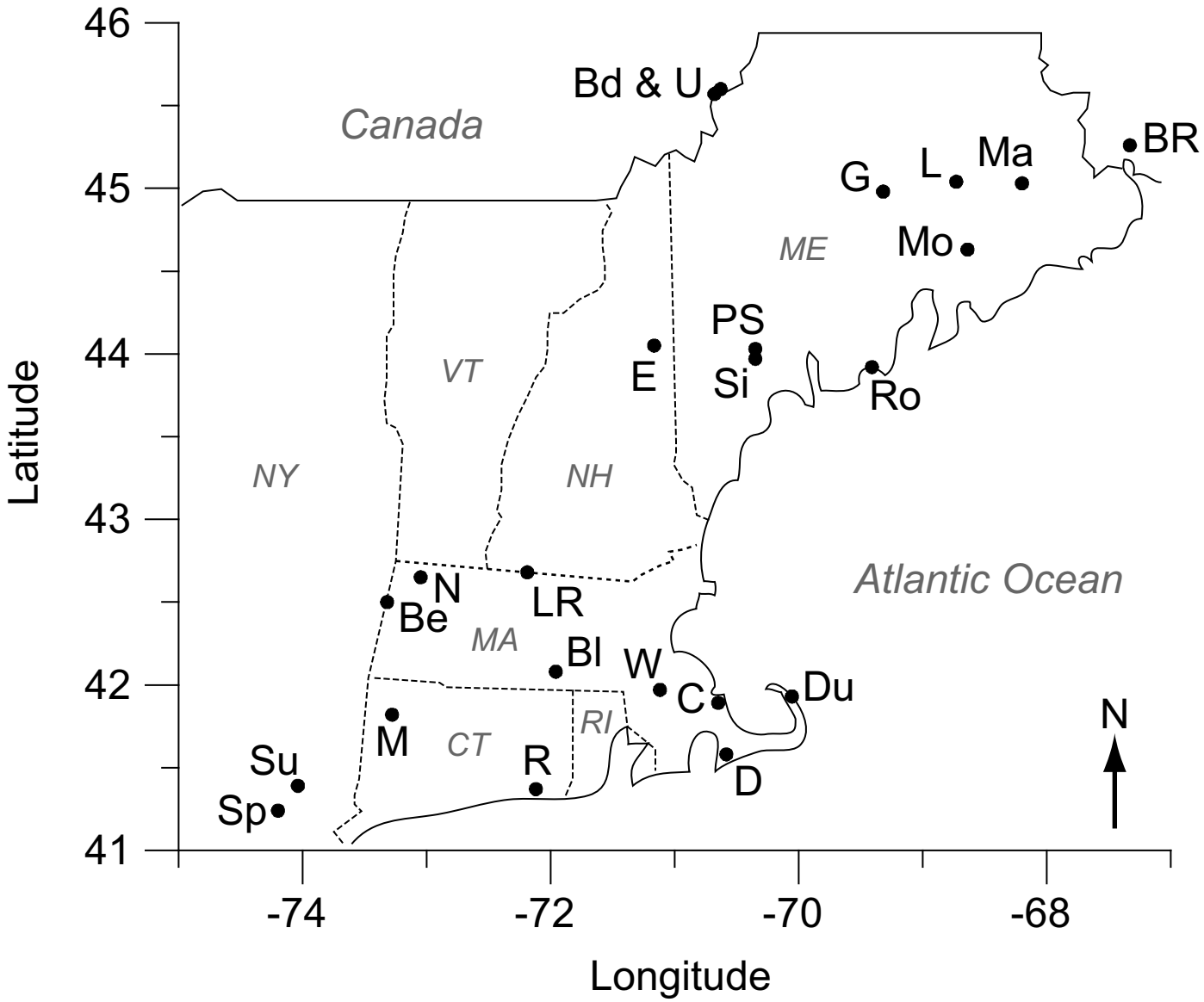
46
45
44
43
42
41
Latitude
-74
-72
-70
-68
Longitude
Canada
Bd & U
BR
G
L
Ma
Mo
ME
PS
Si
E
VT
Ro
NY
NH
Atlantic Ocean
N
Be
LR
MA
Bl
W
C
Du
M
CT
RI
R
D
Su
Sp
N

Figure 2

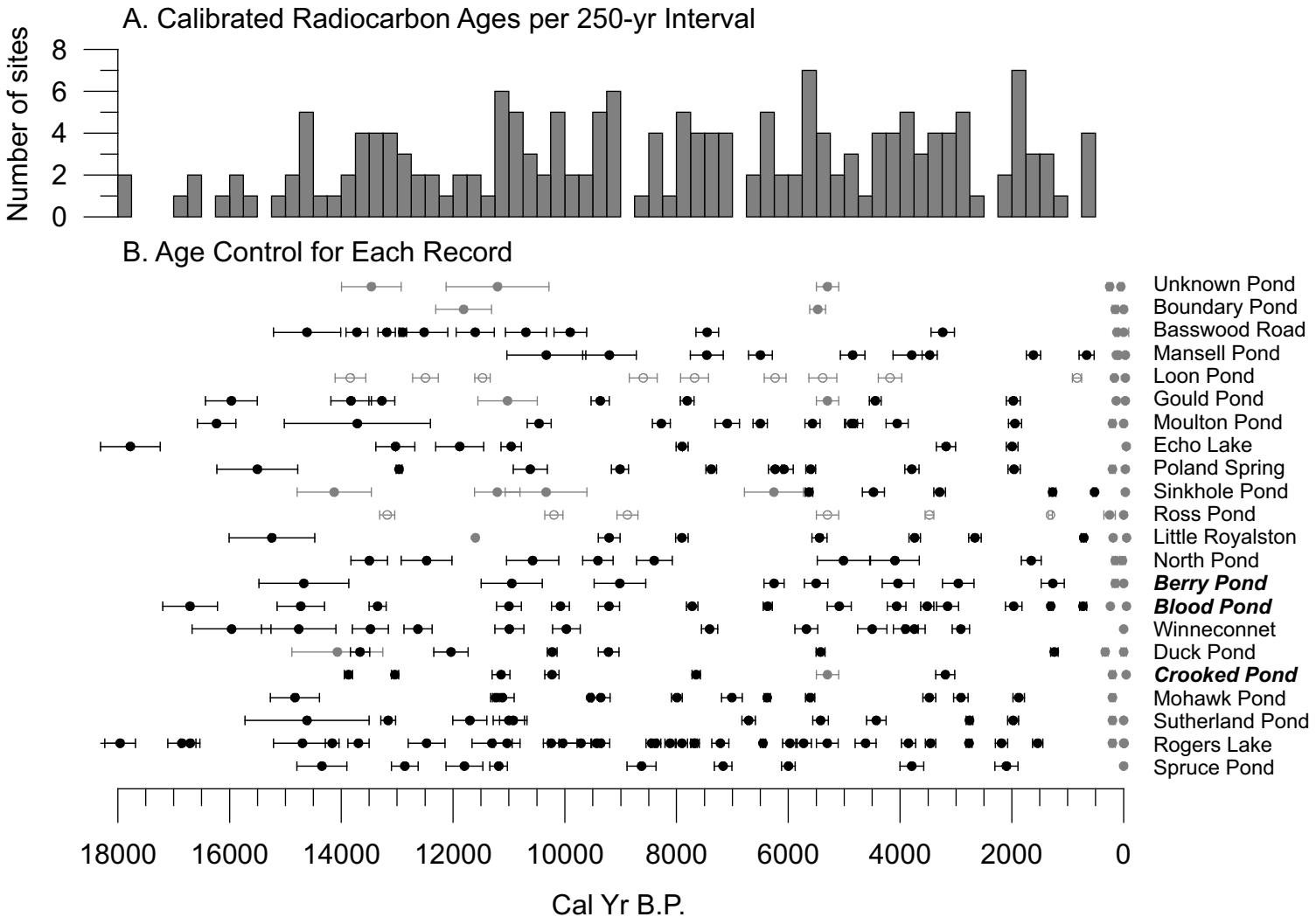
A. Calibrated Radiocarbon Ages per 250-yr Interval
Number of sites
0
2
4
6
8
B. Age Control for Each Record
Unknown Pond
Boundary Pond
Basswood Road
Mansell Pond
Loon Pond
Gould Pond
Moulton Pond
Echo Lake
Poland Spring
Sinkhole Pond
Ross Pond
Little Royalston
North Pond
Berry Pond
Blood Pond
Winneconnet
Duck Pond
Crooked Pond
Mohawk Pond
Sutherland Pond
Rogers Lake
Spruce Pond
18000
16000
14000
12000
10000
8000
6000
4000
2000
0
Cal Yr B.P.

Figure 3

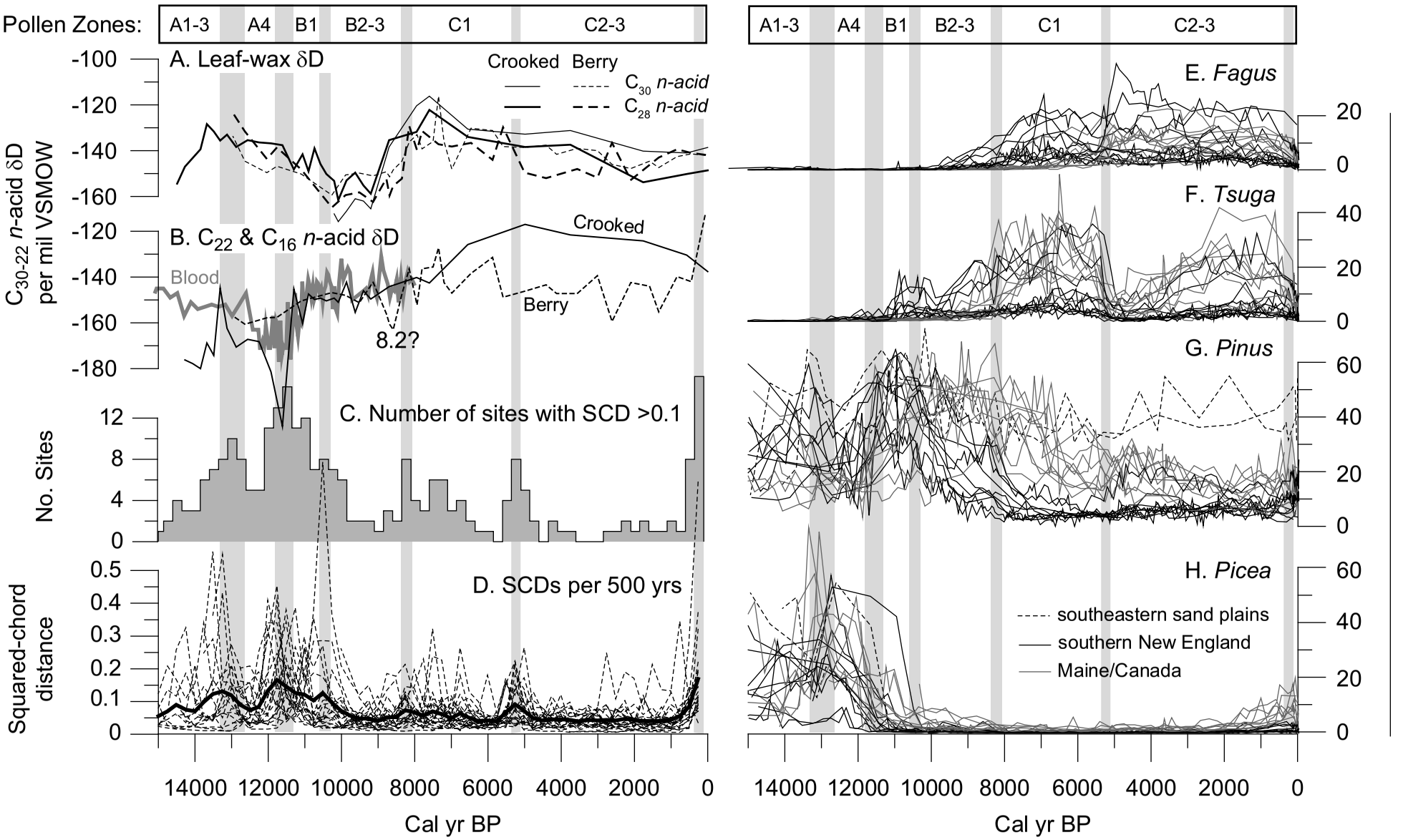
Pollen Zones:
A1-3
A4
B1
B2-3
C1
C2-3
A. Leaf-wax δD
Crooked
Berry
C30 n-acid
C28 n-acid
B. C22 & C16 n-acid δD
Blood
Crooked
Berry
8.2?
C. Number of sites with SCD >0.1
D. SCDs per 500 yrs
C30-22 n-acid δD per mil VSMOW
No. Sites
Squared-chord distance
Cal yr BP
E. Fagus
F. Tsuga
G. Pinus
H. Picea
southeastern sand plains
southern New England
Maine/Canada
Percent pollen

Figure 4

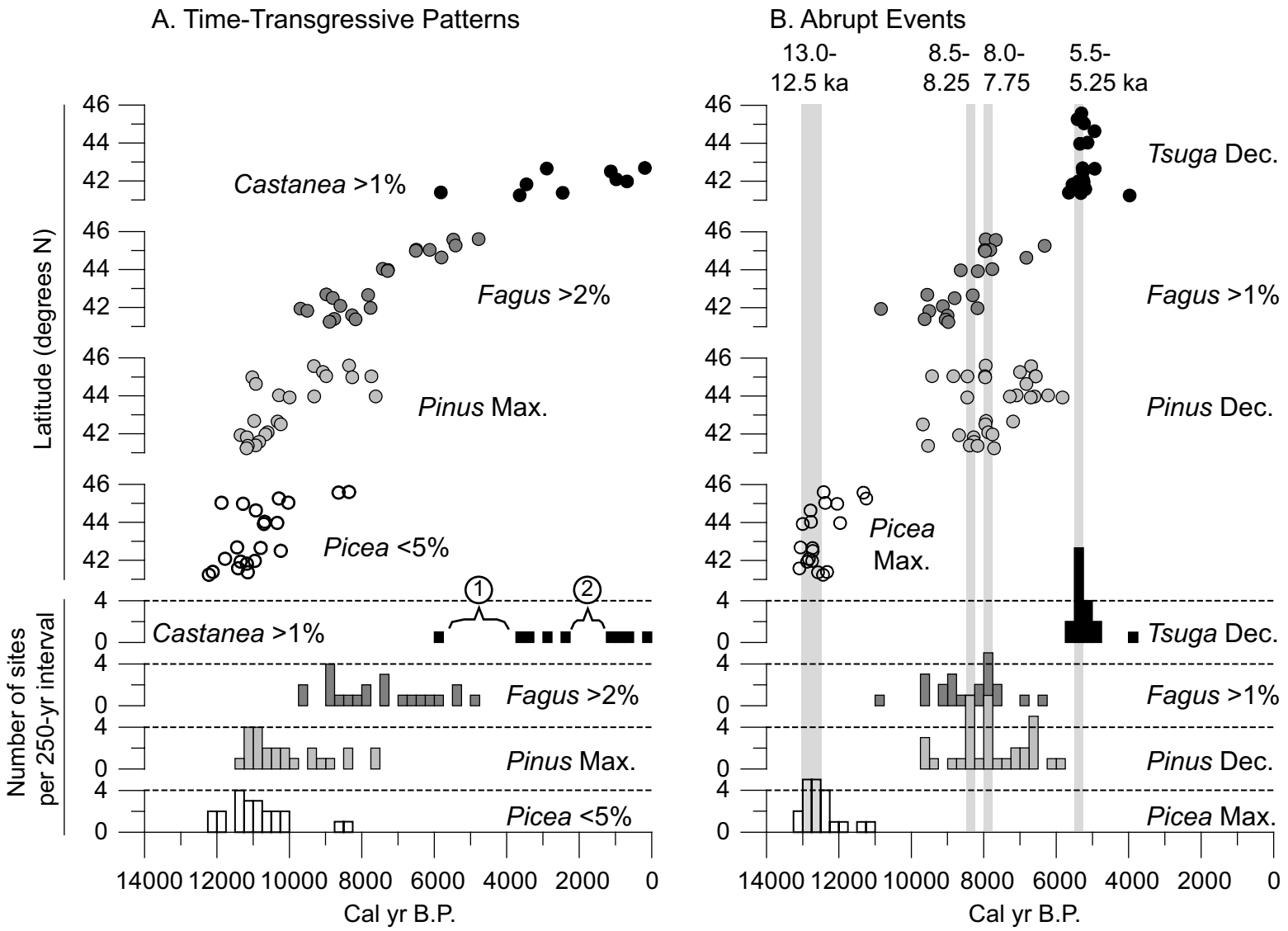
A. Time-Transgressive Patterns
B. Abrupt Events
13.0-
12.5 ka
8.5-
8.25
8.0-
7.75
5.5-
5.25 ka
Latitude (degrees N)
Castanea >1%
Fagus >2%
Pinus Max.
Picea <5%
Tsuga Dec.
Fagus >1%
Pinus Dec.
Picea
Max.
Number of sites
per 250-yr interval
1
2
14000 12000 10000 8000 6000 4000 2000 0
Cal yr B.P.

Figure 5

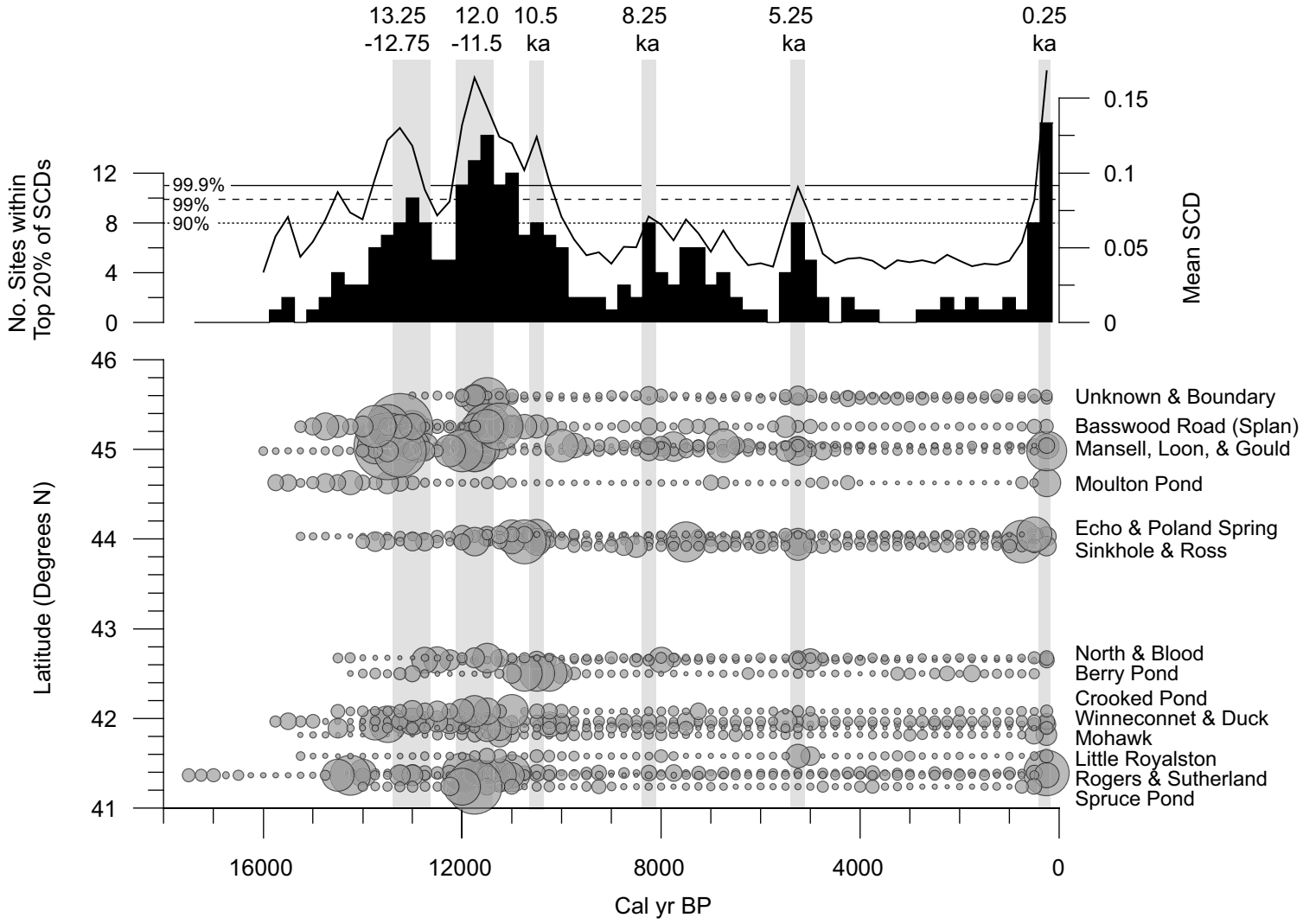
13.25
-12.75
12.0
-11.5
10.5
ka
8.25
ka
5.25
ka
0.25
ka
No. Sites within
Top 20% of SCDs
99.9%
99%
90%
Mean SCD
Latitude (Degrees N)
Unknown & Boundary
Basswood Road (Splan)
Mansell, Loon, & Gould
Moulton Pond
Echo & Poland Spring
Sinkhole & Ross
North & Blood
Berry Pond
Crooked Pond
Winneconnet & Duck
Mohawk
Little Royalston
Rogers & Sutherland
Spruce Pond
Cal yr BP

Figure 6

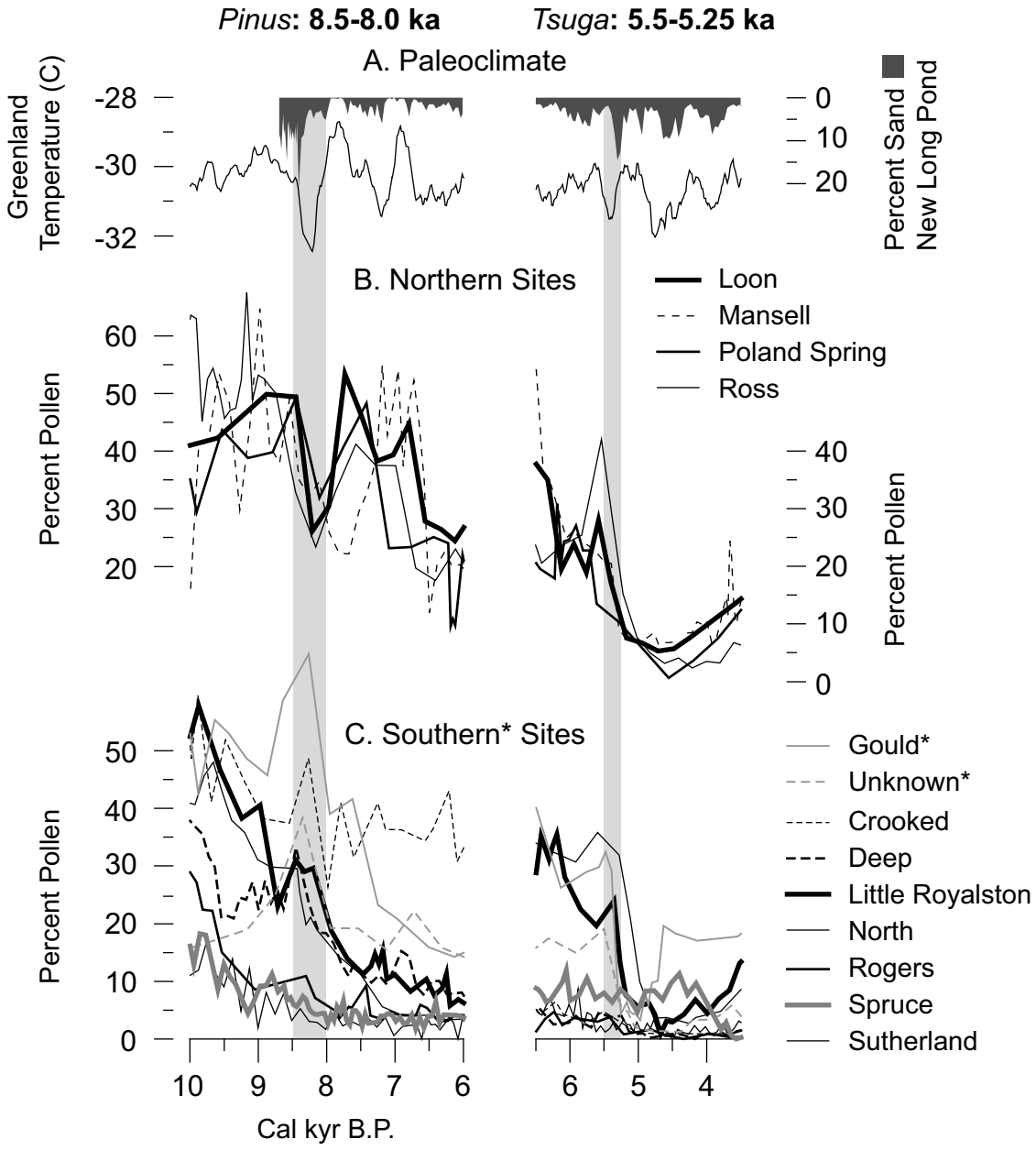
Pinus: 8.5-8.0 ka
Tsuga: 5.5-5.25 ka
A. Paleoclimate
Greenland Temperature (C)
-28
-30
-32
0
10
20
Percent Sand New Long Pond
B. Northern Sites
Loon
Mansell
Poland Spring
Ross
Percent Pollen
60
50
40
30
20
40
30
20
10
0
C. Southern* Sites
Gould*
Unknown*
Crooked
Deep
Little Royalston
North
Rogers
Spruce
Sutherland
50
40
30
20
10
0
10
9
8
7
6
6
5
4
Cal kyr B.P.

Figure 7

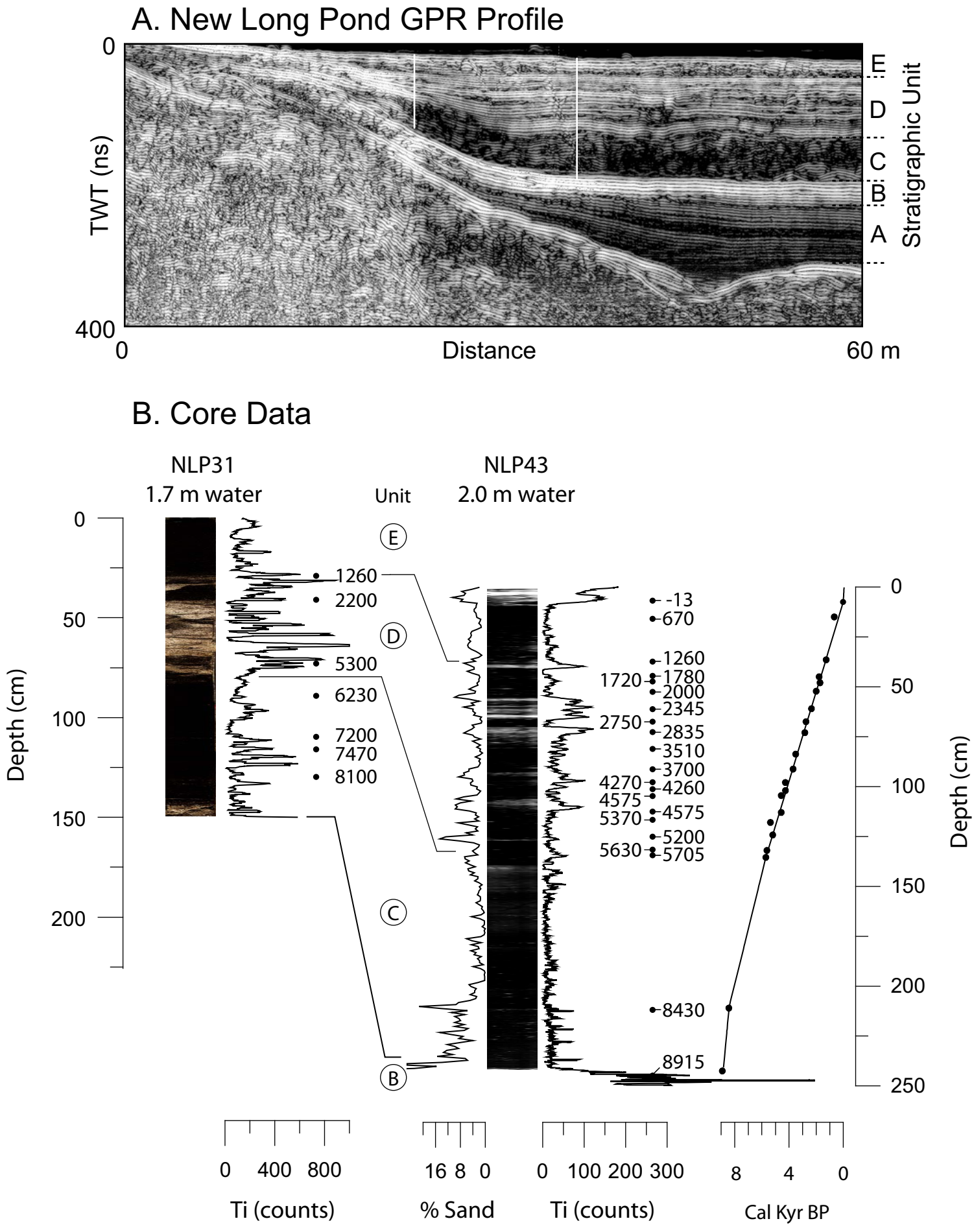
A. New Long Pond GPR Profile
0
400
TWT (ns)
0
Distance
60 m
E
D
C
B
A
Stratigraphic Unit
B. Core Data
NLP31
1.7 m water
Unit
NLP43
2.0 m water
Depth (cm)
0
50
100
150
200
1260
2200
5300
6230
7200
7470
8100
-13
670
1260
1720
1780
2000
2345
2750
2835
3510
3700
4270
4260
4575
5370
4575
5200
5630
5705
8430
8915
0
50
100
150
200
250
Depth (cm)
0 400 800
Ti (counts)
16 8 0
% Sand
0 100 200 300
Ti (counts)
8 4 0
Cal Kyr BP

Figure 8

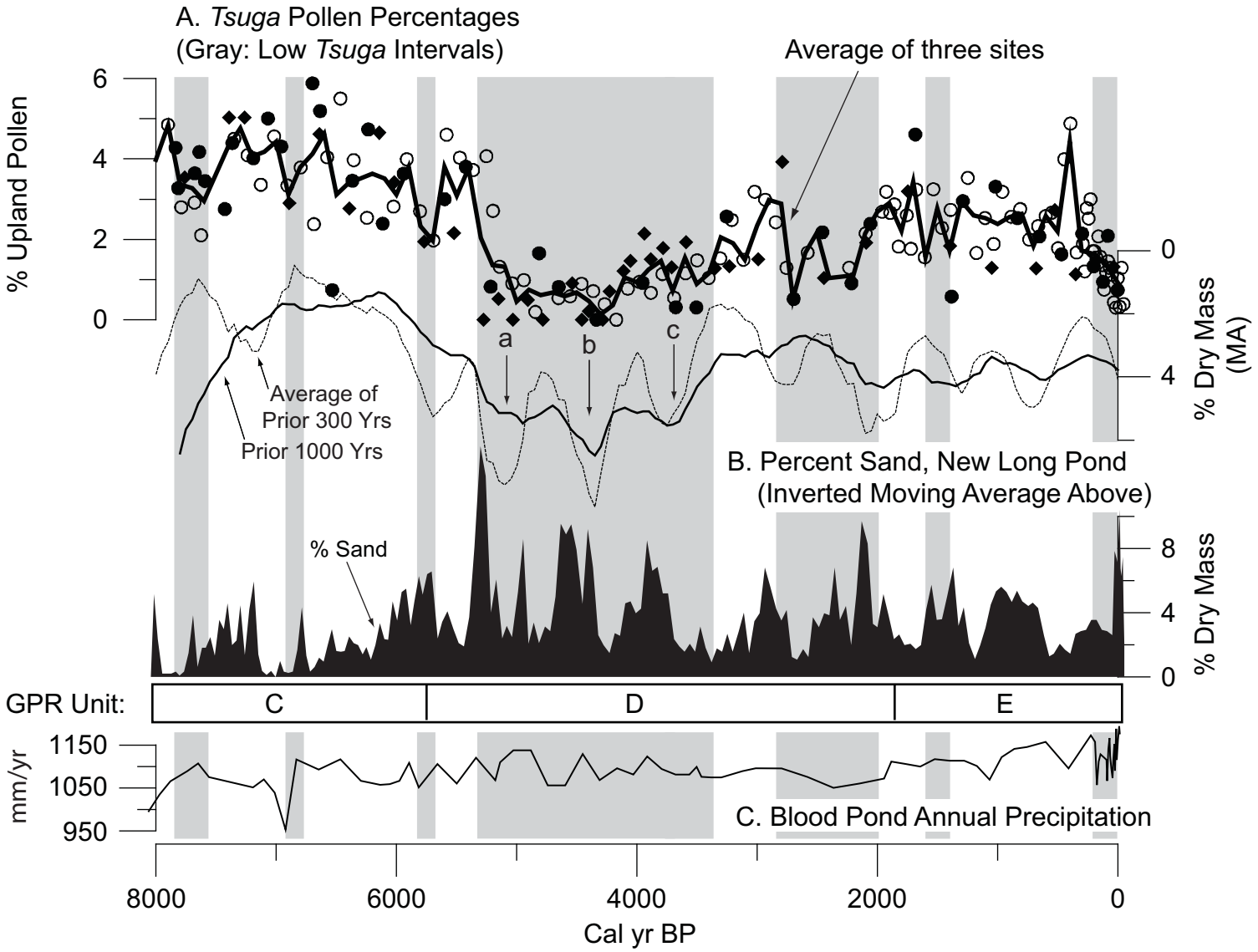
A. *Tsuga* Pollen Percentages
(Gray: Low *Tsuga* Intervals)
Average of three sites
% Upland Pollen
6
4
2
0
a
b
c
Average of
Prior 300 Yrs
Prior 1000 Yrs
0
4
% Dry Mass
(MA)
B. Percent Sand, New Long Pond
(Inverted Moving Average Above)
% Sand
8
4
0
% Dry Mass
GPR Unit:
C
D
E
mm/yr
1150
1050
950
C. Blood Pond Annual Precipitation
8000
6000
4000
2000
0
Cal yr BP

Figure 9

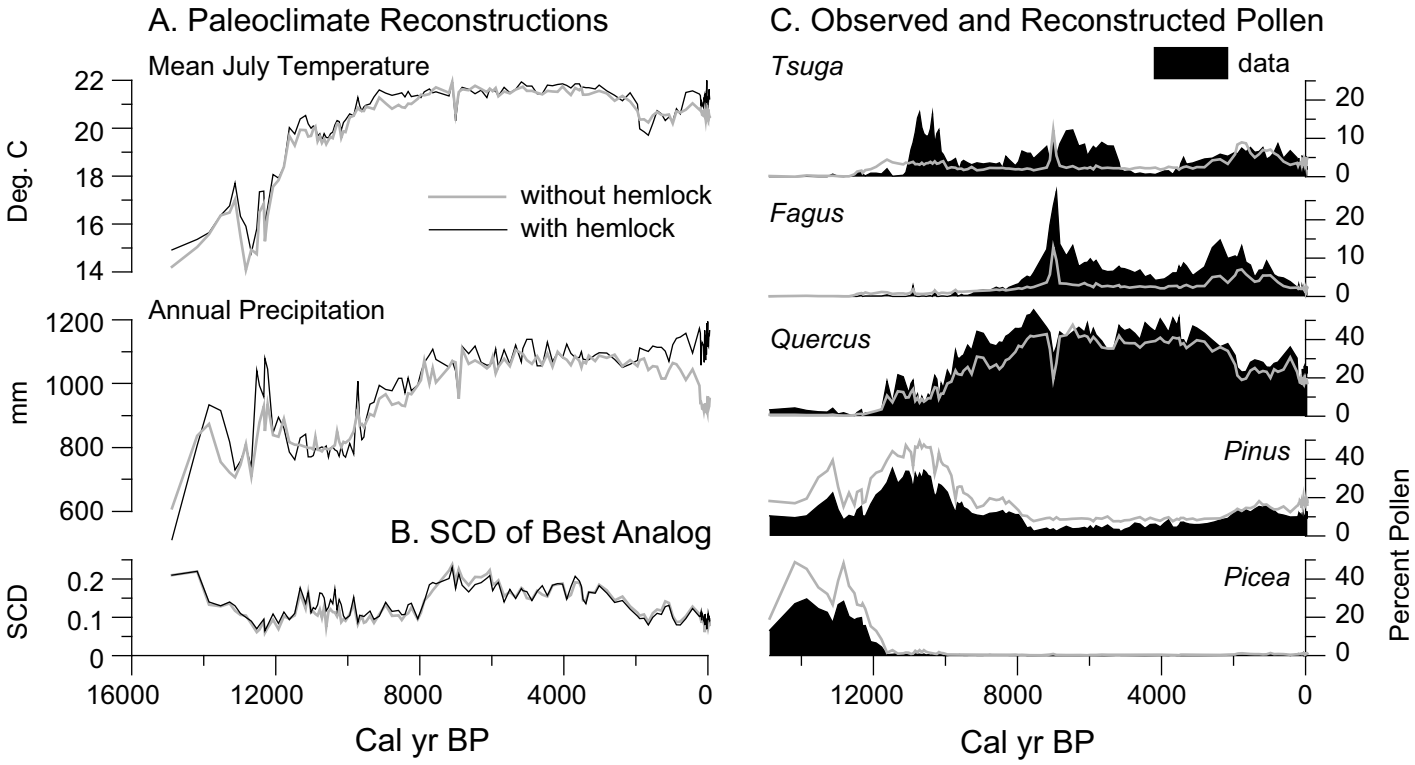
A. Paleoclimate Reconstructions
Mean July Temperature
Deg. C
22
20
18
16
14
without hemlock
with hemlock
Annual Precipitation
mm
1200
1000
800
600
B. SCD of Best Analog
SCD
0.2
0.1
0
16000
12000
8000
4000
0
Cal yr BP
C. Observed and Reconstructed Pollen
Tsuga
data
Fagus
Quercus
Pinus
Picea
20
10
0
40
20
0
Percent Pollen
12000
8000
4000
0
Cal yr BP

Figure 10

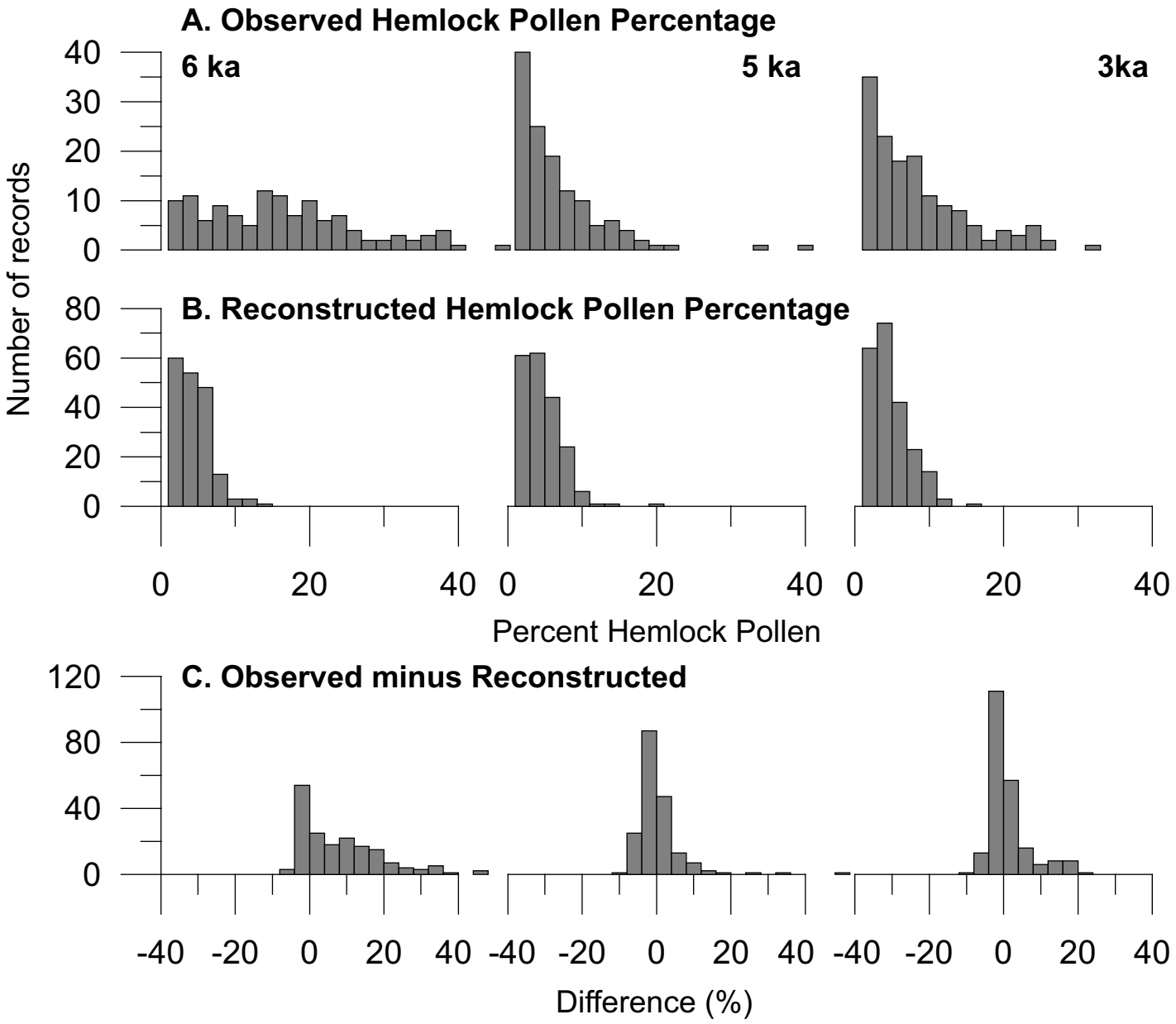
A. Observed Hemlock Pollen Percentage
6 ka
5 ka
3ka
B. Reconstructed Hemlock Pollen Percentage
Number of records
Percent Hemlock Pollen
C. Observed minus Reconstructed
Difference (%)

Figure 11

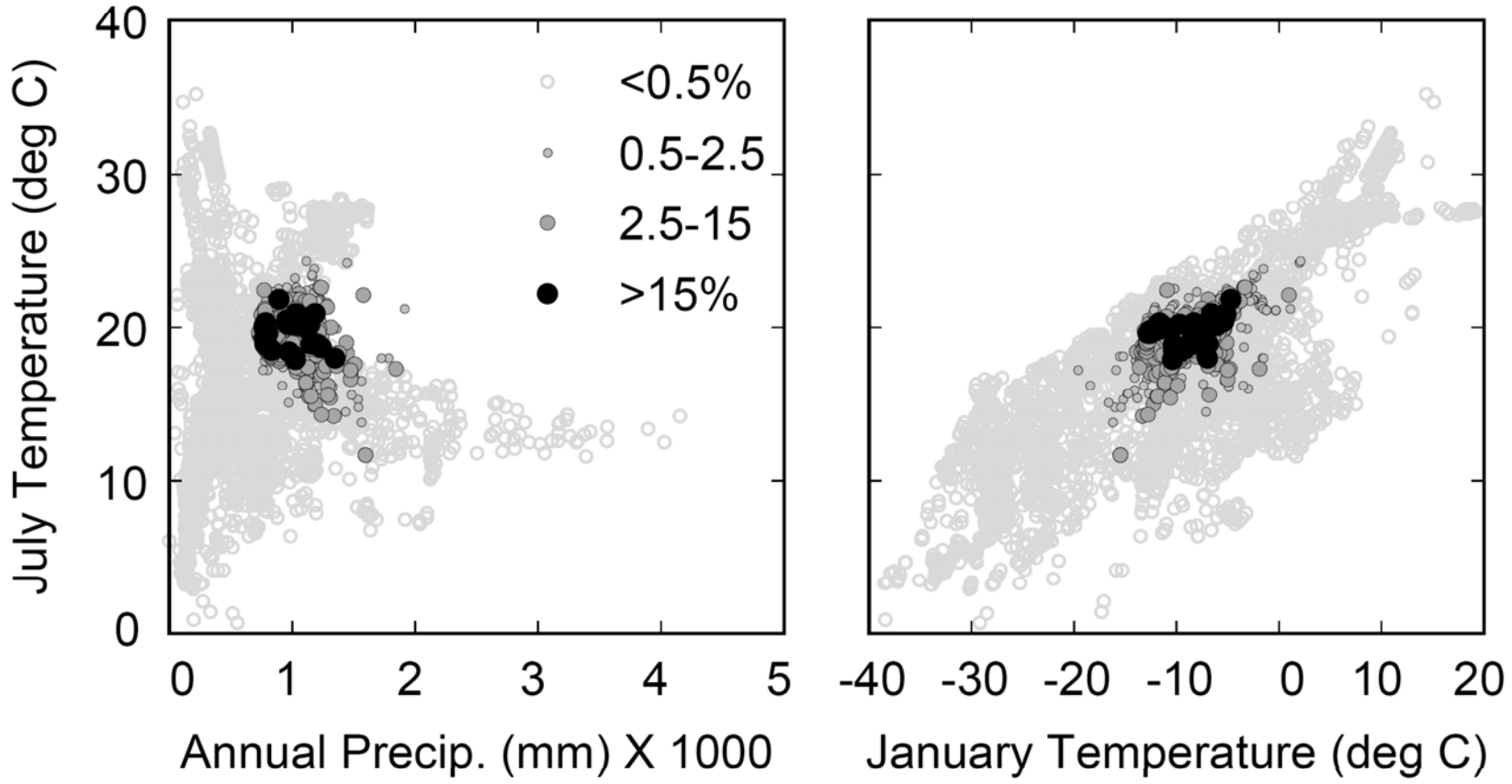
July Temperature (deg C)
40
30
20
10
0
0
1
2
3
4
5
Annual Precip. (mm) X 1000
<0.5%
0.5-2.5
2.5-15
>15%
-40
-30
-20
-10
0
10
20
January Temperature (deg C)

Table 1. Fossil pollen records

Lake	State/Province	Latitude	Longitude	Elevation (m)	Basal Age (cal yr BP)	Number of pollen samples	Samples/ kyr	Source
Unknown (U)	Maine	45.6	-70.63	489	13420	55	4.1	Mott, 1977
Boundary (Bd)	Maine	45.57	-70.68	603	12430	55	4.4	Mott, 1978
Basswood Road (BR)	New Brunswick	45.26	-67.33	106	15230	72	4.7	Mott et al., 1986
Mansell (Ma)	Maine	45.04	-68.73	58	10070	108	10.7	Almquist-Jacobson and Sanger, 1995
Loon (L)	Maine	45.03	-68.20	110	14010	48	3.4	Jacobson et al., unpublished
Gould (G)	Maine	44.98	-69.32	89	16420	73	4.4	Anderson et al., 1992
Moulton (Mo)	Maine	44.63	-68.64	143	16170	33	2	Davis et al., 1975
Echo (E)	New Hampshire	44.05	-71.17	148	11880	25	2.1	Shuman et al., 2005b
Poland Spring (PS)	Maine	44.03	-70.35	94	15489	52	3.4	Jacobson et al., unpublished
Sinkhole (Si)	Maine	43.97	-70.35	95	14700	53	3.6	Jacobson et al., unpublished
Ross (Ro)	Maine	43.92	-69.41	37	14000	75	5.4	Kellogg, 1991
Little Royalston (LR)	Massachusetts	42.68	-72.19	302	15000	88	5.9	Oswald et al., 2007
North (N)	Massachusetts	42.65	-73.05	586	12920	55	4.3	Whitehead and Crisman, 1978
Berry (Be)	Massachusetts	42.5	-73.32	631	14654	42	2.9	Whitehead, 1979
Blood (Bl)	Massachusetts	42.08	-71.96	214	14887	143	9.6	Oswald et al., 2007
Winneconnet (W)	Massachusetts	41.97	-71.12	20	15980	70	4.4	Suter, 1985
Duck (Du)	Massachusetts	41.93	-70.00	2	14000	42	3	Winkler, 1985
Crooked (C)	Massachusetts	41.89	-70.65	28	15000	37	2.5	Shuman et al., 2001
Mohawk (M)	Connecticut	41.82	-73.28	360	15440	44	2.6	Gaudreau, 1986
Deep (D)	Massachusetts	41.58	-70.64	23	15515	130	8.4	Foster et al., 2006
Sutherland (Su)	New York	41.39	-74.04	380	14800	167	11	Maenza-Gmelch, 1997b
Rogers (R)	Connecticut	41.37	-72.12	91	17920	90	5	Davis, 1969
Spruce (Sp)	New York	41.24	-74.20	223	14530	168	11.2	Maenza-Gmelch, 1997a,b

Table 2. Age Constraints on Paleoclimate Evidence

Site	*Evidence shown in Figure 3, 6 or 8*	*Interpolated Age (Calibrated years before AD 1950)*	*Calibrated 14-C Constraints within 500 Years (99% most-probable calibrated ranges) Below*	*Above*
Berry Pond, MA	>7 per mil increase in palmitic acid δD	11,770–11,100		11,342–10,250
	Negative anomally (>10 per mil) in palmitic acid δD	8780–8150	9471–8548	
	>20 per mil increase in leaf-wax δD	8350–8150		
Blood Pond, MA	24 per mil decrease in behenic acid δD	12,559–12,185		
	29 per mil increase in behenic acid δD	11,354–11,235		11,219–10,779
	Negative anomally (>19 per mil) in behenic acid δD	11,156–11,077		11,219–10,779
	Negative anomally (>10 per mil) in behenic acid δD	10,216–10,097		10,235–9919
Crooked Pond, MA	17 per mil decrease in palmitic acid δD	13,310–13,130	13,940–13,790	13,100–12,970
	60 per mil increase in palmitic acid δD	11,615–11,300		11,330–11,010
	>20 per mil increase in leaf-wax δD	9200–7950		7720–7570
New Long Pond, MA	Sand layer attributed to low water levels	8425-8300		8540–8358
	Sand layer attributed to low water levels	5390-5260	5719–5594	5313–4909
	Sand layer attributed to low water levels	4680-4445	5579–5317	4408–4154
	Sand layer attributed to low water levels	3920-3695	4408–4154	3830–3641
	Sand layer attributed to low water levels	2980-2760	3632–3472	2844–2714
	Sand layer attributed to low water levels	2355-2040	2459–2320	2116–1899
	Sand layer attributed to low water levels	1595-1460	1875–1714	1294–1174